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NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* Dr. David A. Boag

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BROOD MIXING BEHAVIOR AND POPULATION DYNAMICS OF CANADA GEESE AT DOWLING LAKE, ALBERTA

by

© WILLIAM MITCHELL GLASGOW

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Brood Mixing Behavior and Population Dynamics of Canada Geese at Dowling Lake, Alberta", submitted by William Mitchell Glasgow in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor

DATE 22 april 1977

This thesis is dedicated to the memory of my father, Robert Ronald Maclean Glasgow, M.D., class of 1934. He kindled my fondness for the outdoors and the wildlife therein, and followed the Dowling Lake Canada goose study with keen interest until his passing on August 30, 1975.

ABSTRACT

The breeding biology and population dynamics of Canada geese nesting at Dowling Lake, Alberta were studied during 1971-1975. The purpose of the research was to examine the factors affecting survival in this population, especially during the brood rearing period.

Breeding pairs did not appear to compete for snow-free locations on the breeding islands in early spring. Territories established during this period decreased in size with the encroachment of later nesting pairs. Nest and territory spacing approached uniformity, but behavioral differences and heterogeneity of the vegetation prevented realization of a statistically significant uniform pattern.

Artificial nesting platforms were constructed to increase the nesting density of Canada geese on the large breeding island. Thirty-five, 39, 20 and 39 percent of the available platforms were used as nest sites in 1971-1974, respectively. Platform nesting success was no different than that of ground nesting geese and there was no significant difference between the territory sizes of platform nesters and ground nesters. Thus platform nesting had no noticeable impact on the Dowling Lake goose population.

Production was affected by nest failure (desertion, predation, unhatched eggs) and gosling mortality. Desertion rates varied from 3 to 22 (mean of 14) percent of the nests. The presence of the gander on the territory was the most important factor in maintaining the territory and thus preventing desertion of the nest site. In three of the four desertions observed, the ganders left the territory for no apparent reason and did not return. Predators destroyed 50 and 46 percent of the nests

in 1968 and 1972, respectively, but had little impact in other years. Unhatched eggs accounted for an average loss of 8.2 percent of those laid in 1970-1974. Mortality in goslings up to 5 days of age averaged 14.5 percent in 1972 and 1973. The mean clutch size was five and the production lost prior to fledging averaged 50 percent; therefore, 100 pairs produced 250 flying juveniles annually.

Brood mixing, where goslings hatched by one pair join the brood of another pair, was prevalent at Dowling Lake. The synchrony of hatching, the tendency to aggregate and the affinity for the same small brood rearing areas facilitated the many interbrood contacts necessary for brood mixing to occur. Forty-three percent of the pairs successfully hatching goslings subsequently lost them to other broods in 1971-1974. Donor goslings were always less than 5 days old but goslings in the recipient broods ranged from 3 to 20 days old. Brood mixing appeared to be a phenomenon resulting from chance encounters between broods, and not the result of dominant geese "stealing" goslings from less dominant pairs. There were no obvious behavioral differences between mixed and single family broods. There was no difference between mortality rates when single and mixed family broods were compared. The impact of brood mixing is not known but possible evolutionary implications were discussed.

Hunting is the major cause of post-fledging mortality. The composite dynamic mortality rate, calculated using 5 years of banding data, was 50 percent annually and indicated a declining population. The population was not declining and theoretical population models were constructed to speculate what might be happening to the population. The recoveries from geese banded at Dowling Lake indicate that Colorado is the major wintering area while Idaho and California are secondary locations.

ACKNOWLEDGEMENTS

I would like to thank David Boag, Ernest Ewaschuk and William Wishart for suggesting that I undertake the study at Dowling Lake. Members of my committee, D. A. Boag, J. O. Murie, W. D. Wishart, E. Ewaschuk, and L. Potash made helpful comments during the design of the study. I am grateful to Dr. T. Narayana for agreeing to replace L. Potash on my committee at a very late date.

The field study was supported by the Alberta Fish and Wildlife Division through W. D. Wishart. I am truly grateful for the many hours of productive discussion with him. I wish to extend sincere thanks to the many members of the Fish and Wildlife Division who helped with the field work, especially Gary Erickson, Ken Froggatt, Charles McNeil, Neil Elle and Ronald Bjorge. Personnel from Ducks Unlimited (Canada) provided invaluable guidance and assistance during the banding drives. Ducks Unlimited (Canada) and the Canadian Wildlife Service made their banding records available to me.

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INTRODUCTION

Many aspects of the natural history and social behavior of Canada geese (Branta canadensis) have been investigated in varying degrees of detail (Kossack 1950, Balham 1954, Collias and Jahn 1959, MacInnes 1962, Sherwood 1966, Raveling 1967, Cooper, 1973, and many others) throughout much of their North American range. Eleven races or subspecies have been identified (see Hanson 1965:13-42, Hine and Schoenfeld 1968, Bellrose 1976:141-164 for subspecific descriptions and distributions), and many authors have emphasized the importance of collecting detailed information on the biology of each race to develop sound management plans for each race and the species as a whole. Raveling (1967, 1969a) suggests that subflocks in wintering areas represent a continued association of geese from the same local nesting area. Thus it is also important to have information on local subflocks of each race rather than treating the race as one large homogeneous flock. The races and subflocks in Alberta have not been extensively studied.

Vermeer (1970), studying Canada geese nesting on islands in southeastern Alberta, determined egg-laying intervals, incubation periods, nest spacing and hatching success. He also suggested that a preference for nesting on islands was a mechanism to counteract mammalian predation. Surrendi (1970) studied behavior, mortality and homing of transplanted juvenile Canada geese. He found that the major daily preflight activity of transplants was feeding, that resident geese were dominant over transplants and that non-breeding resident geese were more tolerant of transplants than breeding pairs. After they attained flight, movements of transplants were localized near the release lake under the leadership of

resident geese, but dispersal from these lakes was immediate if no residents were present. Preflight mortality was 4 percent. Homing to or near their release sites was significantly higher in females than males. McDonald (1975) discussed Canada goose reproduction relative to existing and predicted post-impoundment conditions in the Bow River basin, Alberta. He said the 1971-1972 production was about 175 goslings annually and predicted a severe decrease in post-impoundment production if ameliorative measures were not taken.

Aerial surveys revealed the existence of a large breeding colony of Canada geese at Dowling Lake, Alberta. The Alberta Fish and Wildlife Division made several visits to check nests on the primary breeding island in the lake in 1967. Vermeer (1970) intensively studied the nesting geese on the same island in 1968, and the Alberta Fish and Wildlife Division also made periodic checks of the nests. Noting a high percentage of nest desertion, 18 in 1967 and 27 in 1968, Ewaschuk (1970) investigated in 1969 the possible role of territorial behavior in determining the reproductive success of this population. His study showed that nest desertion was a major factor involved in loss of nests in 1969; the role of territorial behavior in the desertions was discussed. Westworth (1970) continued the study in 1970 with periodic observations and nest checks. The current research at Dowling Lake began in 1971.

Several aspects of the breeding biology of the Dowling Lake Canada goose flock were studied during the breeding seasons of 1971, 1972, 1973 and 1974; these included early spring spacing behavior, territorial behavior, nesting success and success of artificial platform nesters. However, the primary purpose of this study was to monitor post-hatch brood behavior and survival and determine how this affects productivity in this

flock. Brood mixing has been described in populations of Branta canadensis moffitti in the western United States and Branta canadensis maxima in the northcentral United States (Kossack 1950, Miller and Collins 1953, Balham 1954, Geis 1956, Steel et al. 1957, Collias and Jahn 1959, Hanson and Browning 1959, Martin 1964, Brakhage 1965, Sherwood 1966, Hanson and Eberhardt 1971, and others). When one or more goslings hatched by one pair of geese join the brood of another pair of geese, the resultant brood is termed a mixed brood. Ewaschuk (1969, unpublished field notes) and Glasgow (1971, unpublished field notes) both observed several large mixed broods during the 1969 and 1971 breeding seasons at Dowling Lake. Therefore, a major objective of the research was to study how brood mixing occurred and to compare the behavior and survival of mixed broods with single family broods.

THE STUDY AREA

The study area (Fig. 1) was situated near Hanna, Alberta about 320 kilometers southeast of Edmonton. Many lakes and sloughs were present in the depressions created by the rolling topography. The Spondin Lakes (Motz, Mitchell, Dale, Hok, Wolfert, Mattis and James) are all impoundments resulting from earth-fill dams built across natural drainage courses by Ducks Unlimited (Canada). Although the study area lies near the southern edge of the aspen parkland (Bird 1961, Rowe 1972), the grassland plant community dominates with willow (Salix spp.) and aspen (Populus tremuloides) limited to some slough and lake borders. Much of the grassland has been cultivated to produce cereal crops and tame hay with most of the remainder used for livestock grazing.

The Spondin Lakes had small populations of breeding Canada geese associated with them. The Spondin geese, nesting at lower densities, were compared to the more densely nesting flock on Dowling Lake. However, the primary focus for the study was the Dowling Lake area. Dowling Lake, 30 square kilometers in area with 42.5 kilometers of shoreline, is situated 11 kilometers north of Hanna (Fig. 1). A more detailed map of the Dowling Lake study area ($51^{o}42'N$, $112^{o}10'W$) is shown in Figure 2. All the larger lakes in the Dowling area, except Hutton Dam, could be described as astatic saline lakes (White and Hartland-Rowe 1969) with very high turbidity and alkalinity, but many of the smaller water bodies were much clearer and less alkaline. The large island in Dowling Lake (Fig. 3), described in detail by Ewaschuk (1970:3-5, 36) was the most important nesting locality on the lake, but the smaller island (Fig. 4) was also important. The herbaceous cover on the small island was primarily lamb's quarters (Chenopodium album).

Figure 1. The study area.

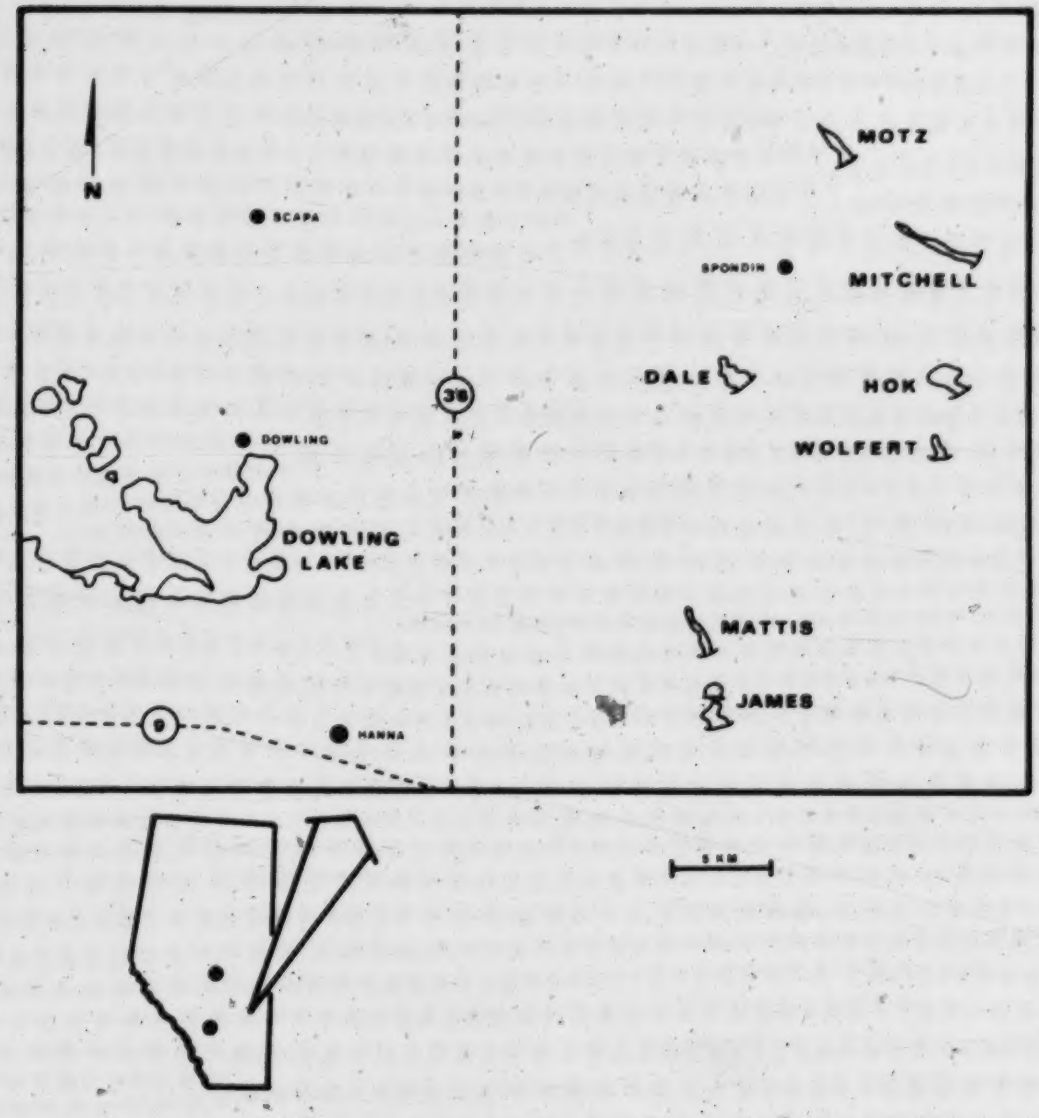

N
SCAPA
SPONDIN
MOTZ
MITCHELL
DALE
HOK
WOLFERT
38
DOWLING
DOWLING LAKE
MATTIS
JAMES
HANNA
5 KM

Figure 2. The Dowling Lake study area.

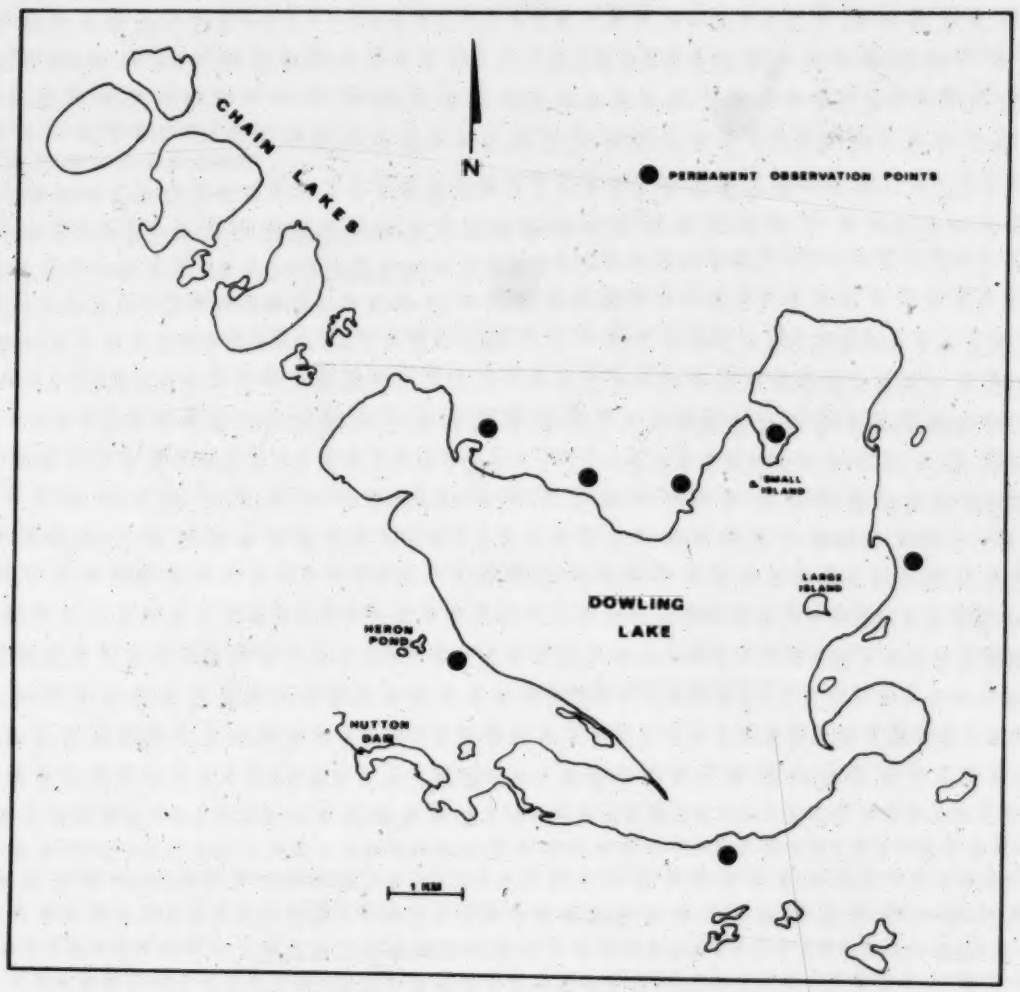

CHAIN LAKES
N
PERMANENT OBSERVATION POINTS
SMALL ISLAND
LARGE ISLAND
DOWLING LAKE
HERON POND
NUTTON DAM
1 KM

Figure 3. The large island in Dowling Lake.

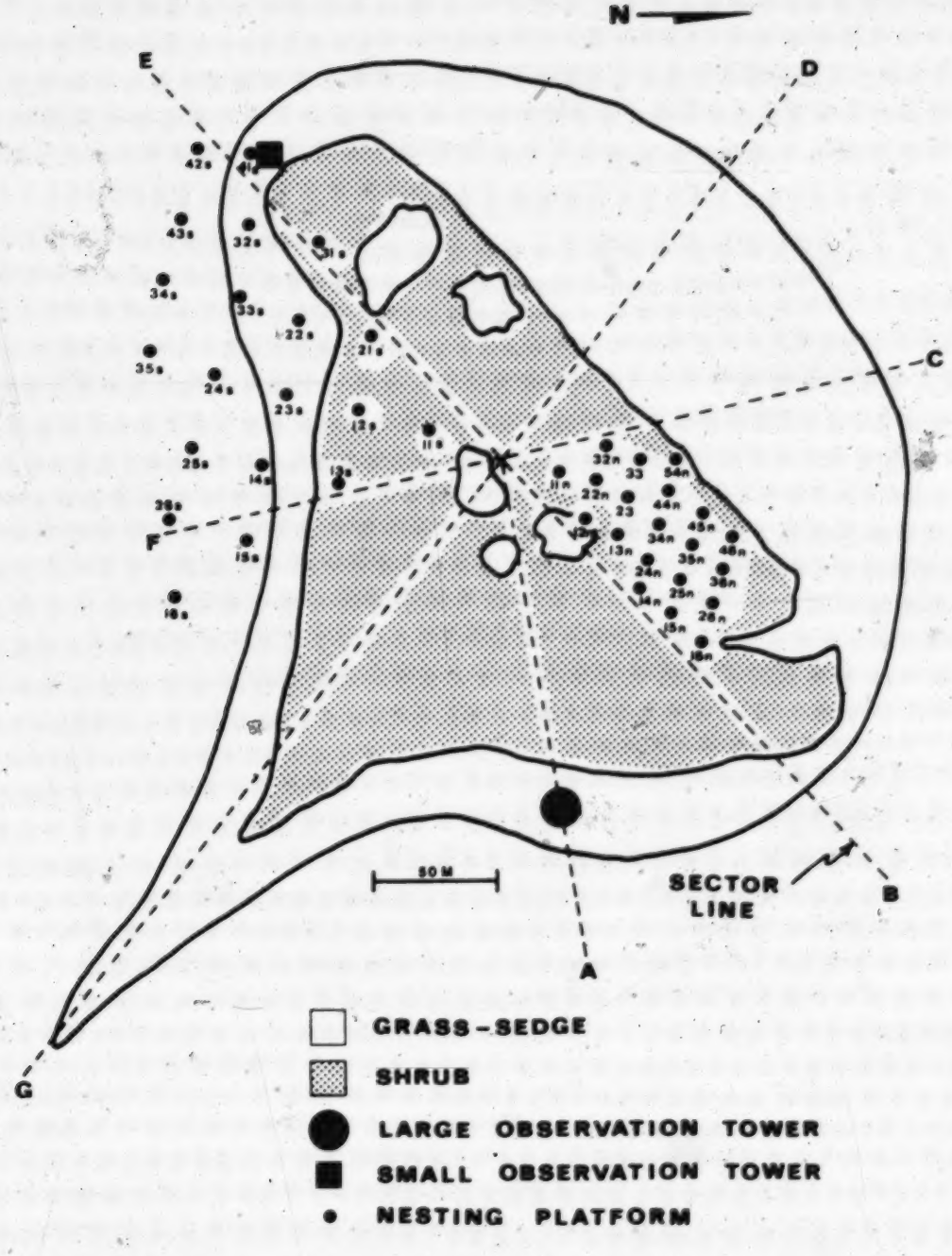
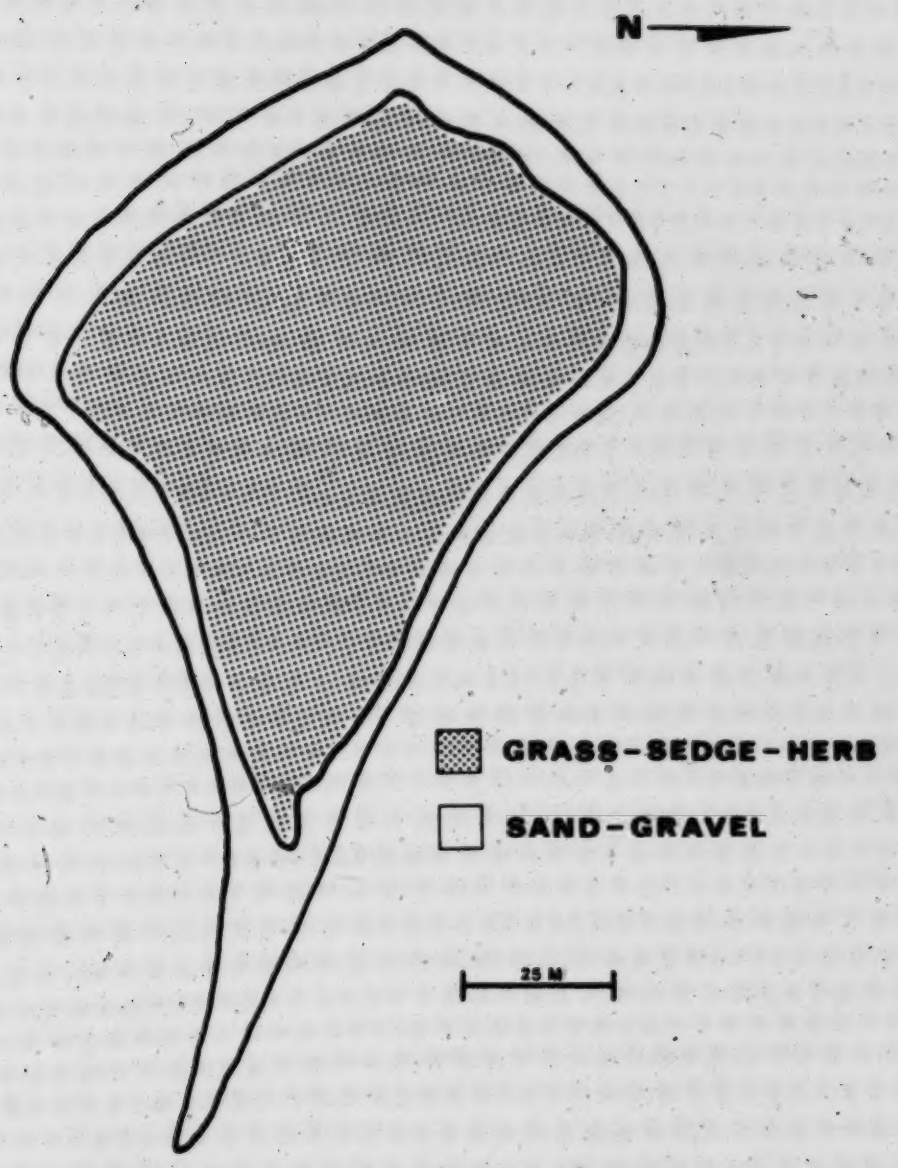

N
E
D
C
F
G
A
B
50 M
SECTOR LINE
GRASS-SEDGE
SHRUB
LARGE OBSERVATION TOWER
SMALL OBSERVATION TOWER
NESTING PLATFORM

Figure 4. The small island in Dowling Lake.


N
GRASS-SEDGE-HERB
SAND-GRAVEL
25 M

METHODS

In 1971 field work was conducted from March 28 to June 4. During the nesting period five visits were made to the large island (Fig. 3) and two to the small island (Fig. 4) in Dowling Lake to determine time of nest initiation, number of eggs laid and the location and fate of the nests. All nests were marked temporarily by stakes (1.2 meter laths) to facilitate measuring distances between them after the hatch was completed. After hatching, the temporary markers (located 3 meters west of each nest) were replaced by permanent markers (numbered aluminum tags on top of 30 centimeter wooden pegs imbedded in the ground about 10 centimeters, just outside the nest rim).

Observations in 1971 were made from the large observation tower (Ewaschuk 1970:7) on the large island on 27 days between April 2 and May 24 representing 252 man-hours. The purpose of the early observations was to determine whether the geese were spacing themselves relative to the snow cover, the vegetation, one another or a combination of these factors. Spatial distribution of the geese on the island was mapped at least twice during each observation day and any behavioral interactions (especially threats and fights likely associated with spacing) were recorded. Mapping was discontinued after snow melt was complete since it was difficult to locate many pairs in the dense vegetation. After nesting began, I recorded the activities of 14 pairs and noted the outcome of interactions between pairs as described by Ewaschuk (1970). One bird was recognizable by the neck collar it bore but the rest were recognized only by their territorial affinities. Similar data also were recorded when possible for the eleven tree and platform nesting pairs visible from the tower. Because the

ganders of these latter pairs often could not be seen from the observation tower, this information was incomplete. During periods of peak activity, only about ten nests could be observed effectively, precluding observations of the platform nests at these times.

The 1972 field season ran from April 1 to July 27. Fifty-one man-hours on 7 days between April 1 and May 12 were spent in the large observation tower during the nesting period. Observations (22 man-hours) were also made from the mainland bluffs southeast of the island. The purpose of these observations was to follow platform use and locate marked adults nesting on the large island. Between April 3 and June 5 the large island was visited 13 times to determine the location, clutch size, stage of incubation and fate of each nest. The small island was visited 9 times during the same period. Clutches of eggs were injected with embryo dyes so the marked broods could be followed later. Each clutch size was marked with a different color. The injection procedures, colors used and the results of using this technique are discussed in Appendix I. When the hatch was completed, all nests were permanently marked as in 1971. The Spondin Lakes were visited twice during nesting to determine location, clutch size and fates of nests.

Brood behavior observations in 1972 were made at Dowling Lake on 32 days between May 11 and July 1 and on 5 days after that until July 27. A Honda trail bike was used for locating broods on the study area. Attempts were made to search the whole area at regular intervals to locate as many broods as possible. I mapped locations of broods and observed them for varying periods of time (usually about 15 minutes). Because of the great amount of time required to cover the entire study area, brood behavior observations were limited to 57 hours during 1972. Permanent observation

points (Fig. 2) overlooked large portions of the potential brooding area and were useful in observing broods without disturbing them. Observations from these points were made with a variable 15-30x spotting scope. Broods were located three times during June on the Spondin Lakes to determine mortality and the extent of brood mixing.

The 1973 field work was conducted from March 23 to July 13. A smaller observation tower (see Fig. 3 for the location), built after the nesting season in 1972, was used in addition to the large tower for observations in 1973. Six days between March 23 and April 30, representing 41 man-hours of observation, were spent in the towers to facilitate identification and location of marked geese. Twenty days (133 man-hours) between May 10 and June 23 were spent in the towers, primarily to observe brood behavior. Nests were observed and marked as in previous years. Nest surveys also were done on the Spondin Lakes. Complete surveys of the study area, with the Honda, were made on 20 days between May 8 and June 25. Six incomplete surveys were also made during this period. Broods were observed for 30 hours during these surveys. Spot surveys (17 man-hours observation) using a truck as an observation point, were made on 9 days between May 25 and July 13. Broods were observed to determine their size and makeup, movements, interactions with other broods, and social behavior within the group. Broods on the Spondin Lakes were observed once during brood rearing to determine the extent of brood mixing.

The major portion of the field work was completed in 1971-1973 but an experiment was conducted in 1974. Nesting progress was checked on April 7 and 22. All the eggs were removed from 24 nests (102 eggs total) on April 23 and taken to be incubated artificially at Brooks, Alberta. Eighty-four eggs hatched and 74 goslings, marked by holes punched in the

foot webs, were subsequently taken to Dowling Lake to be released on the large island on June 4. They were 9 to 15 days old and had had no visual exposure to geese other than themselves. Thirty-six of these were collared during the July 1 banding drive. Observations were made on July 28 and 29 to determine the fate of these marked goslings. Nests were marked and evaluated as in previous years.

Reference will be made throughout this paper to marked or collared geese. Geese were banded annually at Dowling Lake, 1969 to 1974. Each year most of the trapped adults and goslings were marked with individually coded neck collars after Sherwood (1966) and U.S. Fish and Wildlife Service leg bands. A single rivet was added to the Sherwood (1966) design to increase collar retention. Collars were placed on 50 to 75 percent of each year's goslings but a maximum of 15 percent of the adults were marked in any one year. Use of a weak plastic in 1970 resulted in a 100 percent collar loss that year. Sightings of marked birds indicated collar retention was greater than 75 percent during other years.

Most of the statistical comparisons between data were made using a chi-square test or t-test (Sokal and Rohlf 1969). Other tests, used infrequently, are indicated in the body of the thesis. Statistical cohorts were considered significantly different when the probability level was less than or equal to 0.05.

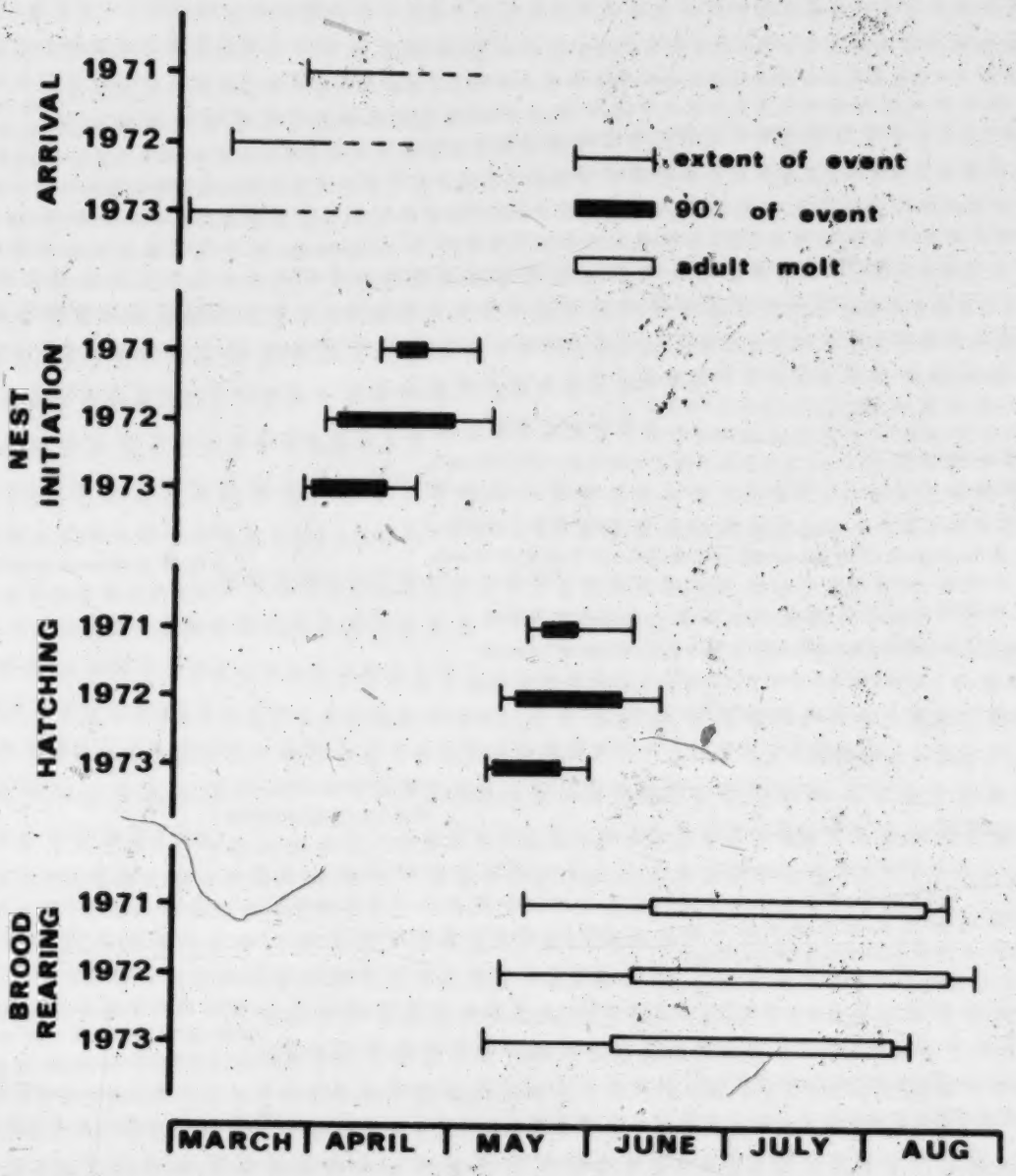
RESULTS AND DISCUSSION

A. Chronology of Events During the Breeding Season of Canada Geese at Dowling Lake, 1971-1974

The timing of arrival, nest initiation, hatching, rearing of broods and molting of adults is illustrated in Figure 5. Data were insufficient to include 1974 in the figure. The timing of these events in 1967, 1969, 1970 and 1974 was not monitored accurately, but they appear to resemble the situation in 1971. Vermeer's (1970) description of the 1968 breeding season suggests it was similar to 1972.

The population of Canada geese nesting at Dowling Lake does not arrive synchronously as suggested for other populations (Bellrose 1976:158). The first geese seen were on the large island (Fig. 3) on March 28, 1971; March 11, 1972; March 1, 1973 and March 29, 1974. Fewer than 10 individuals were seen at these times. Lincoln (1950) suggested that Canada geese move northward following the 1.7°C isotherm. Earliest arrivals at Dowling Lake could be correlated with the severity of the winter and onset of spring snow melt which began when daily air temperatures exceeded 1-2°C. For example, 1974 was the most severe winter with deep snow and cold temperatures well into March; hence the latest arrival during the 4 years. Newly arrived geese were observed on the nesting island over a period of about 3 weeks each year. Since most geese had initiated nests by the end of this time, I assumed that all members of this population had arrived. However, the presence of large numbers of migrants made it difficult to tell when the last of the Dowling Lake birds had arrived. Based on a sample of 33 marked adults and 21 marked 2-year-olds, I was unable to distinguish any particular order of arrival in terms of age. Adults were

Figure 5. Chronology of reproductive events for Canada geese at Dowling Lake in 1971-1973.


ARRIVAL
1971
1972
1973
extent of event
90% of event
adult molt
NEST INITIATION
1971
1972
1973
HATCHING
1971
1972
1973
BROOD REARING
1971
1972
1973
MARCH
APRIL
MAY
JUNE
JULY
AUG

always among the earliest arrivals but no age cohort predominated. These observations were not consistent with the suggestion by Balham (1954) that older birds arrive first. Three of nine marked pairs, known to have raised goslings the previous year, returned to the nesting grounds accompanied by their marked broods. The fate of the other six broods was not known.

Nest initiation began, on average, 19 days (range 11-27) after arrival (Fig. 5). Initiation was recorded when the first egg was laid in a scrape. Although arrival was relatively asynchronous, nest initiation in most years was relatively synchronous (Fig. 5). Heavy coyote (Canis latrans) predation in 1968 (Vermeer 1970) and 1972 and egg removal in 1974 probably led to renesting by many pairs. The disturbance that I caused, while dyeing embryos in 1972 (Appendix I), may have been an important addition to predation in stimulating renesting in that year. The renesting likely contributed to the prolonged nest initiation period in those years. Eggs were laid at a rate of 1 every 1.5 days until the clutch was complete. Down appeared in the nest at about the time the fourth egg was laid. Nest attentiveness increased during laying until the onset of incubation with the laying of the last egg. Based on 74 nests, the incubation period averaged 27.8 days.

The first broods were seen on May 16, 1971; May 11, 1972; May 8, 1973 and May 18, 1974. The hatching peak (90 percent of the nests) occurred during the week the first brood was seen, even in 1972 and 1974 when the periods of nest initiation and hatching were much longer. This synchrony in hatching had important implications for brood mixing which will be discussed later. The brood-rearing period (hatching to fledging) was about 68 days. Mixed broods with goslings of different ages did not fly away

from the lake until the youngest birds were able to take wing.

Figure 5 illustrates the duration of the adult flightless period. Adults with broods molted the flight feathers about 4 weeks after the hatch and remained flightless for 4 to 5 weeks. Thus they had regained flight just before the young but did not usually fly unless disturbed. Most of the nonbreeding geese flocked together with broodless adults and left the Dowling area between May 25 and June 25 in 1971-1974. I assumed they took part in the annual molt migration of Canada geese as described by Sterling and Dzubin (1967), but there are no band returns or sightings to substantiate this. Band returns (courtesy of the Canadian Wildlife Service and Ducks Unlimited, Canada) indicate these molt migrants are in central Alberta in early to mid-September and migrate out of the province about the same time as adults with their young. Whether they rejoin the Dowling Lake flock either at the breeding lake or elsewhere is unknown.

B. Early Spring Spacing Behavior of Breeding Geese

The spacing of nests and therefore territories was studied by Ewaschuk (1970) at Dowling Lake in 1969. He found nest spacing tended towards uniformity and suggested that the spacing would have been more uniform had the vegetation that influenced it not been so heterogeneous. His data on spacing was gathered after the breeding season was over. The spacing problem was investigated further in 1971 to see if and how previous nest site tenacity, arrivals of more breeding geese and differential snow melt were affecting the size and location of territories. Information on nest site tenacity was also obtained from 1972 to 1974.

The first geese to arrive at Dowling Lake, 1971-1974, were often singles, pairs or groups of less than ten, followed by larger flocks during peak arrival from late March to early April. Small groups and flocks fragmented very quickly into smaller groups (threes, pairs and singles), often on the same day as arrival. Most of the adult geese (2 years or older) appeared paired on arrival and separated very quickly from the larger groups. The gander defended a relatively undefined area wherever the pair was at any particular time; this "moving territory" was first described in geese by Jenkins (1944). Fidelity to territories of previous years was not obvious during the first few days after arrival as pairs often occupied areas more than 100 meters apart on consecutive days. These activities occurred when most of the nesting habitat was still snow-covered so that the cues for location of previous territories may not have been visible, or perhaps the geese were not ready to settle at a fixed location. Location of territories and nest sites for 22 marked birds is discussed in the following paragraphs.

Four marked pairs of geese, for which a previous history was known, returned to breed at Dowling Lake in subsequent years. One pair was observed in 3 consecutive years and three pairs were observed in 2 consecutive years. All four pairs used the same territory they had occupied the year previously. The female of the pair observed in 3 years used a different nest site each year but all were within 4 meters of one another.

Three marked females lost marked mates and returned the following year with new mates. Two of these (both with unmarked mates) nested in the same area as the previous year (one in the same nest bowl and one 3 meters away). The other female paired with a 2-year-old male hatched at Dowling Lake, and attempted to return to her territory of the previous year, but the male was unable to hold any territory and she did not nest that season. Two marked ganders, with known mates that were lost and replaced, returned to the same territories the following year. The new females both established different nest sites than their previous mates.

Of six marked females mated to unmarked males, five were known to nest in 2 successive years and one in 4 successive years. Two of the five nested in the same territory (one in the same bowl and one 5 meters away), but the other three females nested 296, 189 and 159 meters away from their previous nests. The sixth female nested the first two years in the same nest, moved 159 meters in the third year and another 84 meters in the fourth year. Three marked ganders were paired with females of unknown status. Two of these remained on the same territory while the other established a territory about 100 meters away in the successive year.

These data represent a rather small sample but suggest that both adult males and females exhibit territorial fidelity from year to year. However, they also illustrate that the status of the mate is important and that

changes in territorial location and status can occur. Data were insufficient to determine if age and dominance status were involved in movements; the fact that a 2-year-old male was not able to establish a territory suggests that they are important. It was also evident that, although females choose the nest site, returning adult males choose the location of the territory. Thus spacing and territorial establishment are affected by previous experience and territory or nest-site tenacity.

Accurate mortality estimates for the population of geese nesting at Dowling Lake are not available, but mortality rates among juvenile Canada geese around Brooks (150 kilometers south of Dowling Lake) were 49 percent (Surrendi 1970). Adult mortality is lower than that for juveniles and may be as low as 30 percent (Grieb 1970). Since 77 percent (17 of 22) of the geese at Dowling Lake returned to the same territory the following year but only 70 percent of the geese survived, about 54 percent of the territories from the previous year are reused by the same geese. This leaves considerable room for birds with previous breeding experience to move around and newly recruited breeding pairs to move in. Their spacing is obviously affected by factors other than site tenacity.

Three known family groups and several marked pairs accompanied by one to three other geese established themselves on or near the pair's previous territory. In all cases these "family" individuals were tolerated very near the pair but other geese were not. This tolerance near the pair decreased until sometime during laying after which no geese were allowed within the territory. Thus yearling females, when they reach reproductive age, may be attracted to nest in the same area as their parents. Unfortunately, marked birds were not available to test this hypothesis.

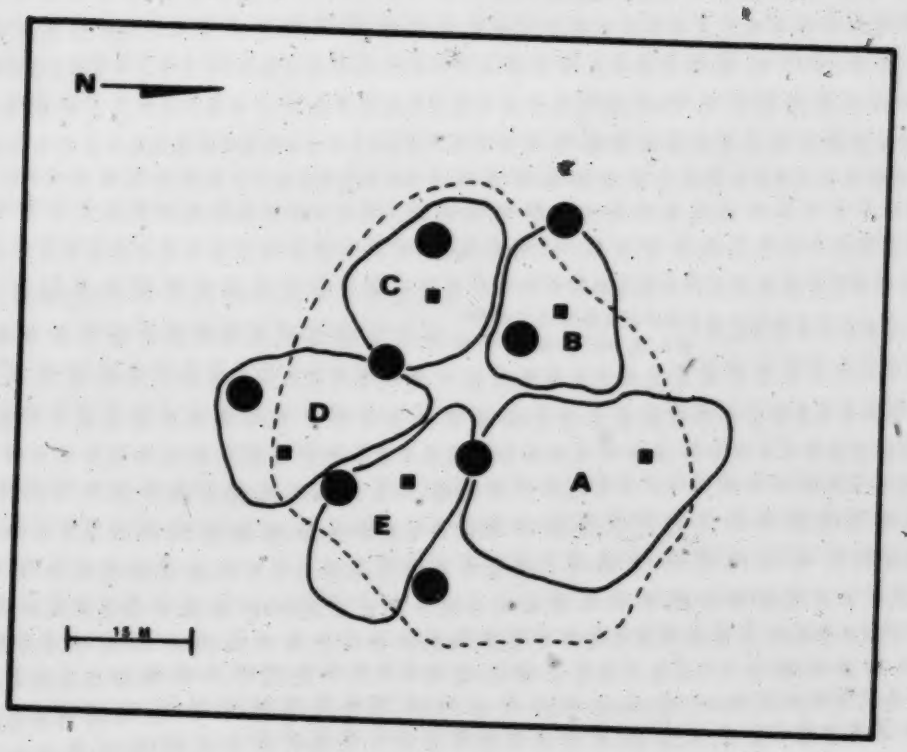
Barry (1967) said that arctic-nesting species of geese, lesser snow geese (Anser caerulescens caerulescens) and black brant (Branta bernicla nigricans), showed intraspecific competition for early available snow-free nesting habitat which affected the distribution and spacing of nests. Since all or most of the island was covered with snow when many of the breeding geese arrived at Dowling Lake, the possibility that snow cover might affect territorial behavior and subsequent nest spacing was investigated in 1971 and 1972. The geese were plotted twice daily on maps of the nesting island to determine their spatial distribution relative to each other and the snow-free versus snow-covered areas. The geese, even when they numbered less than 10 pairs, were spaced well apart on top of the snow-covered island. The earliest snow-free areas allowed nest initiation as much as 2 weeks before the latest nesters, but there was no indication of strong competition for snow-free locations. Many geese, including marked older pairs, defended territories on top of the snow, nesting only after suitable snow-free sites were available. A chi-square test for independence comparing pairs per snow-free area and pairs per snow-covered area showed no significant difference over time. Spacing remained relatively uniform over the whole island regardless of the location and extent of snow-free nesting habitat. However, in 1974 after collection of this data had ceased, there was an unusually heavy snowfall and slow spring melt. Deep snow forced many pairs to abandon a traditional nesting area in the tall willows just west of the large observation tower on the large island in Dowling Lake. This may have caused the lower numbers of nests recorded in that year but I was unable to confirm this because the clutches in a number of nests had been manipulated. Snow melt was primarily important in determining when different pairs nested

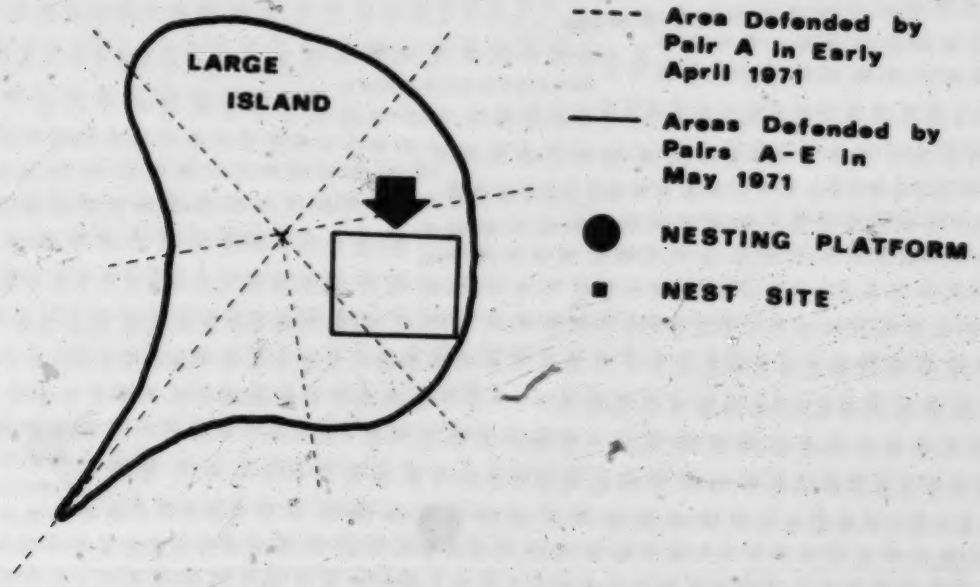
but did not apparently affect nest dispersion in 1971 and 1972. The results for 1974 are equivocal on this point.

Arrival of additional breeding pairs and growth of dense vegetation as snow melt progressed were important in determining the size and location of the territory. Since 54 percent of the population returned to traditional territories located all over the island, the rest of the breeding geese had to establish territories in the intervening space. Early in the season defended areas were often much larger than later when only the area around the nest was defended. For example, one pair initially defended a snow-covered area including six artificial platforms (Fig. 6). The arrival of more breeding pairs, as the snow melted and uncovered the dense vegetation, decreased the size of the area that the original pair could defend. The original area eventually supported four additional territories with nests (Fig. 6). It seems likely that the inability to patrol such a large area and keep other pairs out forces a reduction in the size of the territory. Ewaschuk (1970) showed that nests were significantly closer together in dense vegetation and suggested that the screening provided by the vegetation was the important factor preventing defense of a larger territory. This was also apparent in 1971. The vegetation was an effective visual screen but also interfered with movements of the gander, reducing the area he could cover. There was also a tendency for the gander to concentrate his defense around the focal point of the nest after its initiation regardless of the vegetation type.

Thus, behavior before nest initiation seemed less important to the final spatial distribution of nests than did traditional use of territories and nest sites and the ability of a gander to defend such sites adequately. There did not appear to be any competition for snow-free areas over snow-

Figure 6. Defended area of a pair of Canada geese on the large island in Dowling Lake in 1971, comparing the early April and mid-May time periods.


N
C
B
D
A
E
15 M


LARGE
ISLAND
Area Defended by Pair A in Early April 1971
Areas Defended by Pairs A-E in May 1971
NESTING PLATFORM
NEST SITE

covered areas. The time between arrival and availability of snow-free nest sites, critical for arctic-nesting geese (Barry 1967), was not important to Canada geese nesting at Dowling Lake. Hence the apparent selective advantage for early nesting arctic geese does not hold for prairie geese.

C. Territorial Behavior, Nest Dispersion and Hatching Success

Territorial Behavior

During the 1971 nesting period several aspects of behavior were noted to allow comparison with the study of Ewaschuk (1970) in 1969. The emphasis of observation was placed on outcome of interactions between pairs.

The results of interactions, involving 14 pairs under close observation, were classified in the same manner as Ewaschuk (1970) except that ties were not recorded because they were difficult to evaluate. The nests and territories of the 14 pairs under close observation are indicated in Figure 7. The results of interactions involving these pairs are summarized in Figure 8. Four of the 14 clutches were deserted before hatching; the other 10 were successfully hatched. In the four desertions, pairs K and L lost significantly more interactions than they won, pair M won all interactions observed which was only three and pair H won and lost about equal numbers of interactions (Fig. 8). Most of the interactions involved the ganders. Females generally were involved only if their ganders were absent or had just been driven off the territory. Details of the desertions are presented in the following paragraphs.

Pair L was totally dominated by the gander of pair A and was driven off before incubation began. This was the only case where a pair was driven off together by a gander after they had established a nest. Breeding pairs are generally dominant over a single goose and thus territorial pairs are not often driven off by another gander.

Pair H won and lost about equal numbers of interactions, however, after the nineteenth day of incubation, the gander left and did not return. The adjacent gander drove the female off in the absence of her mate. The

Figure 7. Nest sites and territories of the 14 pairs of Canada geese under observation in 1971.

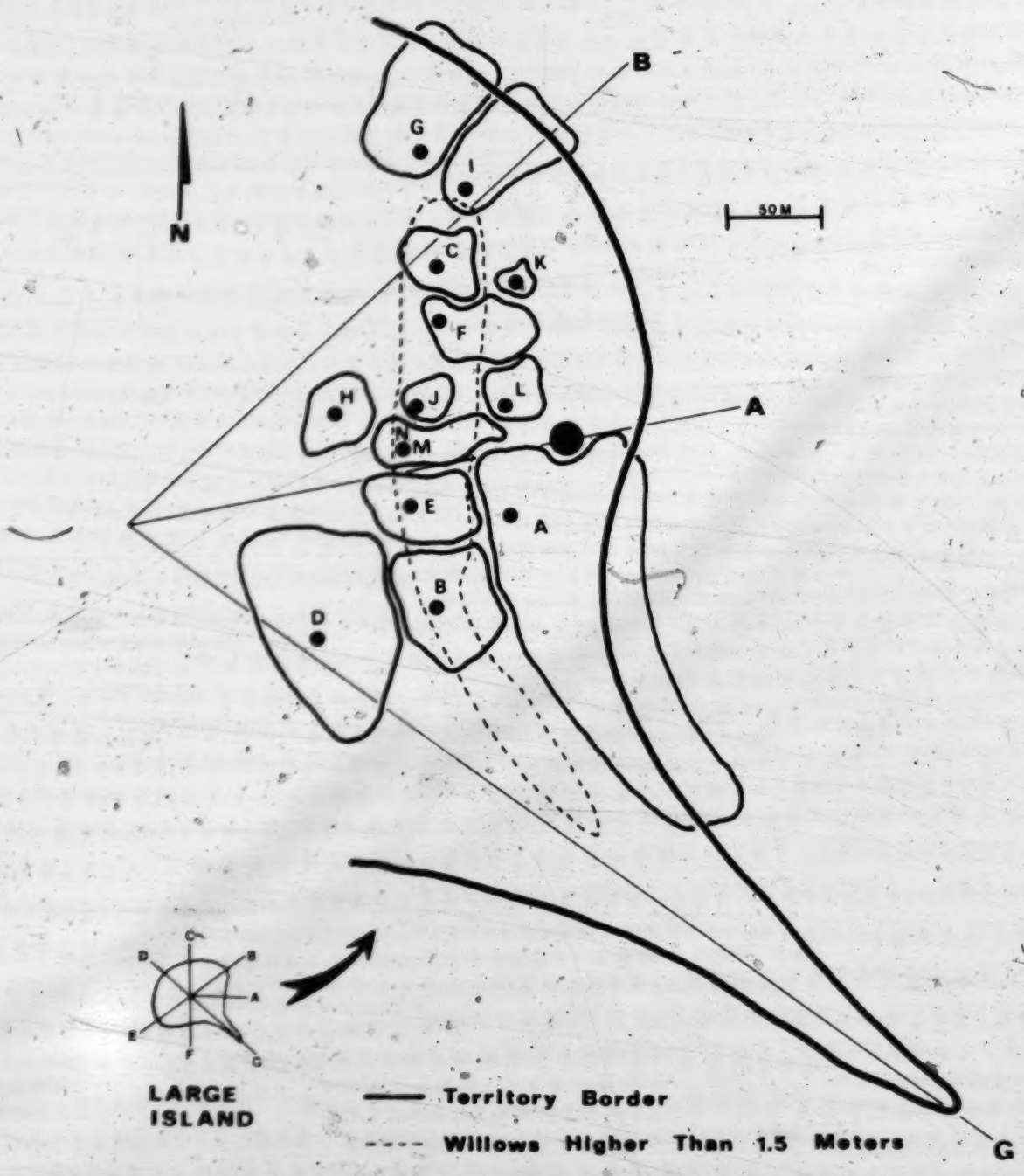
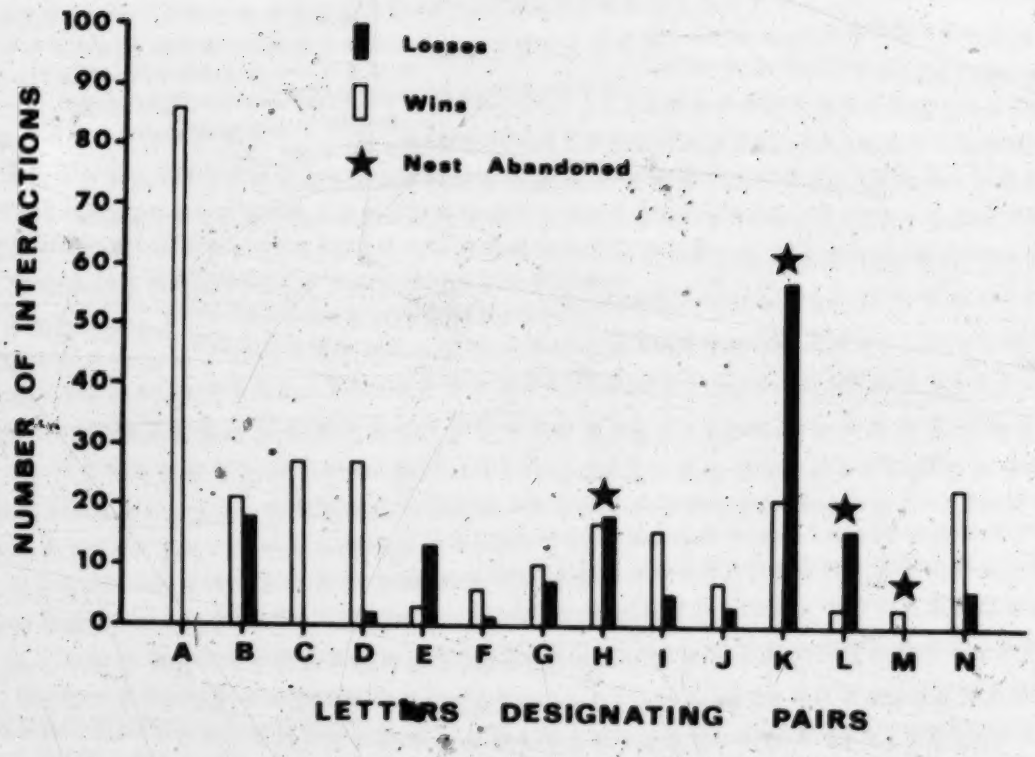

B
G
I
N
50 M
C
K
F
H
J
L
A
M
E
A
B
D
C
D
B
A
E
F
G
LARGE
ISLAND
Territory Border
Willows Higher Than 1.5 Meters
Observation Tower
Nest Site
G

Figure 8. Numbers of interactions for the 14 pairs of Canada geese under observation in 1971.


Losses
Wins
Nest Abandoned
NUMBER OF INTERACTIONS
100
90
80
70
60
50
40
30
20
10
0
A B C D E F G H I J K L M N
LETTERS DESIGNATING PAIRS

female tried repeatedly to return but was constantly repelled by the adjacent gander. She did not return after the second day. Nest K was established by a 2-year-old female after nest L was abandoned. Pair K was not observed to interact with any of the other breeding geese but had a very small territory about 12 meters in diameter. Their nest was in the middle of an area heavily used by non-breeders. Many of the non-breeders were paired and engaged in interactions with pair K so the gander of K was under constant pressure. The gander was sub-dominant to most of the non-breeding pairs which made this pair exceptional. The female initiated 23 percent of the territorial defense actions and most of the wins (Fig. 8) occurred when she was involved. No other females were ever seen to initiate a territorial defense action (a walking- or running-threat display). After 18 days of incubation the gander left for 6 hours and the female was driven off by non-breeders. A California gull (Larus californicus) destroyed two of the five eggs but the female returned with her gander and continued to incubate. The following day the gander left again, the female was again driven off and a California gull ate the remaining three eggs. The pair were not seen again.

The gander abandoned territory I but the nest was well hidden from the nearest neighbors so the female was not disturbed and hatched the clutch successfully.

Nest M was 1.7 meters above the ground in an old heron (Ardea herodias) nest in the willows. It was directly above nest N which was on the ground. Pair M held no territory on the ground and the M gander spent all his time "on territory" right at the nest site. He won all three interactions in which he was observed. The female left after 13 days incubation and did not return. The gander remained at the nest site for 3 days but

when she did not return he deserted the nest site. This was not the usual desertion pattern.

The 28 percent desertion rate for the 14 nests under observation was not significantly higher than that for the whole colony, 14 percent. The mean nearest nest distance for deserted nests, 13.2 meters, was significantly less than that for successful nests, 17.2 meters, in 1971. There was no significant difference between these two in 1972 but the overall success was greatly reduced by coyote predation which may have affected the results. The mean nearest nest distance for deserted nests, 11.3 meters, was again significantly less than that for successful nests, 17.7 meters, in 1973. Ewaschuk (1970) also found the mean nearest neighbor distance for deserted nests was significantly less in 1969.

The presence of the gander on the territory seemed to be the single most important factor in nesting success as found by Collias and Jahn (1959) and Ewaschuk (1970). Behavioral interactions that were lost were not the only factor involved in a male abandoning his territory since other males had proportionately as many losses but did not desert their territories (Fig. 8). The territory size was smaller around the deserted nests but once again many pairs with small territories (not observed but inferred by nearest nest distances) were successful nesters. Geis (1956) and Brakhage (1965) suggested that the "attentiveness" or fidelity to the territory may be a function of age and experience. Younger ganders are less likely to be attentive and hence successful. Geis (1956) assumed and Brakhage (1965) showed a progressively lower clutch size with decreasing age. Thus, if deserted nests were mainly those of young geese, the clutch size in them should also be lower.

Deserted nests in 1971 had a lower mean clutch size (5.0) than successful nests (5.7) but the difference was not statistically significant. However, in 1972 and 1973 deserted nests had a significantly lower clutch size (4.1 and 4.4, respectively) than successful nests (6.7 and 5.2, respectively). Further evidence that younger, less experienced birds may be involved in desertions was that only three of six known 2-year-old females nested successfully in 1971 and 1973. They were all nesting for the first time, and if their ganders were of similar age (this seems likely), they would also be inexperienced. No 2-year-old ganders were known to hold territories at Dowling Lake in 1971 to 1974. One known 3-year-old male held a territory during 1973 and his female nested in platform 11n (Fig. 3). This gander formed some kind of mutual tolerance or perhaps sub-dominant bond with the adjacent gander whose territory included the ground space below 11n. These ganders often stood less than 3 meters apart but usually displayed nothing more than mild threats toward one another. On occasions when they did fight the gander of 11n always lost but the female was never harassed, perhaps because she was on the platform.

Although the evidence suggests that "attentiveness" of a gander may well be associated with experience, Collias and Jahn (1959) have evidence that at least one experienced nester remained unsuccessful over a period of several years. Ryder (1967) found that Ross' goose (Anser rossii) males graze on the territory and do not show as much weight loss as females. It may be that younger birds or habitual "losers" can only establish poor territories in terms of food potential and ease of defense. If so, the ganders become so run down before the end of incubation that they are forced to leave the territory. Perhaps continued harassment by neighbors does not allow much time for

feeding regardless of the potential food supply.

Unsuccessful nesters may be a combination of habitual "losers" and inexperienced birds, but the data were insufficient to establish the actual cause of gander desertions in this study.

Nest Densities and Dispersion

Nesting densities on the larger 6.5 hectare island in Dowling Lake were 14.8, 19.7, 16.9, 14.3, 14.9, 16.9 and 17.8 per hectare in 1967-1973 respectively. Ewaschuk (1970) said about one-fourth of the island's total area was mud flat leaving about 4.9 hectares of habitable space; this would increase the densities recorded to range between 19.0 and 26.1 nests per hectare.

Vermeer (1970) found that the pattern of nest dispersion on the larger island in Dowling Lake showed a significant deviation from randomness in the direction of uniformity in 1968. Ewaschuk and Boag (1972) found the pattern on the same island tending toward uniformity but the deviation from randomness was not significant (i.e. $P>0.05$) in 1969. Both used the Clark and Evans (1954) nearest-neighbor test. The data collected in 1971-1973 were subjected to both the Clark and Evans test and the Campbell and Clarke (1971) test for non-randomness using nearest-neighbor distances. The latter test showed a very significant deviation from randomness ($P<0.01$) for all years and the former showed a non-significant deviation toward uniformity similar to Ewaschuk and Boag (1972). Vermeer (1970:235) said; "the tendency toward uniform spacing may result from the strong territoriality observed in this species." Ewaschuk and Boag (1972) agreed but suggested that the heterogeneity of the vegetation may have been more

effective in modifying this pattern in 1969 when the nesting density was lower, and thus the non-significant deviation from randomness. My data supports Ewaschuk and Boag (1972) since nest distribution in years with greater numbers of nests (e.g. 1973) was either much closer to uniform distribution (Clark and Evans 1954) or more significantly non-random (Campbell and Clarke 1971) than those years with fewer nests.

The percentage of nests initiated within each of the seven sectors on the large island during 1970-1973 is shown in Table 1. There was no significant change in the percentage of nests initiated within any sector during the 4 years except in sector DE where 1971 was different from the other years. This suggests a rather constant response to the different vegetative cover types within different sectors despite the changing density of breeding geese. The reason for the 1971 change in sector DE is not known. Ewaschuk (1970:38) said, "larger territories were generally more open with respect to vegetative cover than smaller ones." This was also found in 1970-1974. The area encompassing a gull colony, consisting of several thousand ring-billed gulls (Larus delawarensis) and a few hundred California gulls, occupied about 33 percent of the potential nesting cover but supported less than 8 percent of the goose nests in 1971-1974. The open cover accounted for the greater distances between nests, but large areas of the gull colony were not used by the geese, suggesting that the gulls were having some inhibitory effect on the geese. It is also possible that gulls were destroying some goose nests and taking over these sites before I could find them. The gulls nested much later than the geese but arrived at the same time and were on territories when the geese commenced nesting.

Ewaschuk (1970:39) showed an inverse correlation between vegetative

Table 1. Distribution of Canada goose nests on the large island in Dowling Lake.

Location	1970		1971		1972		1973	
	No.	%	No.	%	No.	%	No.	%
Sector AB	12	13	14	15	13	12	14	12
BC	10	11	16	17	19	17	20	17
CD	8	9	6	6	5	5	6	5
DE	24	26	12	12	29	26	24	21
EF	21	23	27	28	30	27	28	24
FG	6	7	11	11	4	4	8	7
GA	10	11	11	11	10	9	16	14
Total	91	100	97	100	110	100	116	100

cover at the nest site and numbers of interactions involving pairs of geese and their neighbors and suggested, "that dense vegetation may act as a 'screen' thus reducing the visual stimulus for another bird to attack." Ganders would be forced to concentrate their activities around the nest site where auditory signals and some visual contact could be used to defend the territory, but territory sizes would be smaller than those in open vegetation. This hypothesis is supported by the high nesting densities recorded (Table 1) in the dense vegetation in sectors DE and EF.

Nesting densities on the smaller 0.8 hectare island in Dowling Lake (Fig. 4) were 3.8, 3.8, 10, 6.3 and 3.8 nests per hectare in 1969 and 1971-1974 respectively. This island had a colony of about 100 pairs of California gulls and 20 pairs of common terns (Sterna hirundo) in all years observed. The vegetation was very similar to that in the gull colony on the large island. These densities were significantly lower than densities on the large island as a whole but were similar to those in the gull colony on the large island. However, nearest neighbor distances were much shorter on the small island than in the gull colony on the large island suggesting that factors other than vegetative cover and the gulls were important in nest spacing. Closer examination revealed that the topographic relief acted as a screen between many of the nest sites on the island and probably acted in an analagous manner to vegetative screening on the large island, but territories were still large because most included part of the flat, open shoreline.

Nest dispersion on the small island was very uniform for all years when nests were recorded (1969, 1971-1974). The small island had a uniform open cover type consisting mostly of grasses and forbs such as lamb's quarters. The gulls trampled the lamb's quarters over most of

the small island early in the season. Subsequent growth was rank and over-wintered plant skeletons were common. During the spring of 1972 over-wintered plant skeletons were more abundant than other years and may have resulted in the significantly higher number of nests, 9, when compared to the average, 5, for all years.

Density and dispersion of nests were difficult to determine for the geese nesting on the Spondin Lakes. In 1972, 27 nests were located and in 1973, 18 were located. It is evident that Canada geese in the Hanna area have a strong preference for nesting on islands (Ewaschuk 1970, Surrendi 1970, Vermeer 1970, this study). Islands are in short supply and quite small on most of the Spondin Lakes. Therefore, density and dispersion on and between water bodies were very likely controlled by the location and number of natural islands and artificial nesting structures available. Only one nest was found on a mainland site during this study. Hok and Dale (Fig. 1) had potential insular nest locations that were not used. Behavioral observations showed that they were not used because ganders from adjacent sites were holding these as part of their territories. Nests were much more widely spaced here than on the island in Dowling Lake indicating perhaps a reduced tolerance to neighboring geese. All insular sites were used on the other five Spondin Lakes.

Hatching Success

Fates of Canada goose nests on the two islands in Dowling Lake for the 1967-1974 breeding seasons are presented in Tables 2 and 3. Table 4 records the fate of nests on the Spondin Lakes. Successful nests were those hatching at least one egg. Abandoned nests were those in which the eggs were deserted regardless of cause. Nests completely destroyed by predators were placed in the third category and nests whose fate was uncertain were placed under "unknown".

Predation reduced the production of the goose colony very significantly in 1968 and 1972 (Table 2) but was unimportant in the other 6 years. Canada geese nesting in the Hanna area show a strong preference for island sites, presumably to avoid mammalian predation (Ewaschuk 1970, Vermeer 1970). In 1968 and 1972, coyotes were responsible for most of the predation (Vermeer 1970, this study). The coyotes gained access to the large island in Dowling Lake when low water levels exposed mud flats connecting it to the mainland in 1968 (Vermeer 1970). Warm temperatures in March 1972 caused an early disappearance of snow on the island and allowed nesting to start earlier than the previous five years. The warm early March temperatures were followed by much colder weather in later March and early April that retarded melting of the lake ice, especially between the large island and the mainland. The resultant ice bridge was used by the coyotes to cross to the island. As the ice melted on both the island and mainland shores, the coyotes swam across progressively wider expanses of water until they were swimming the entire distance of 180 meters. Coyotes were observed on the island on three different occasions in 1972; twice a pair and once one individual. The same female, marked through hair peculiarities

Table 2. Fates of Canada goose nests on the large island in Dowling Lake.

Year	Nest Fate: Successful No.	Successful %	Abandoned No.	Abandoned %	Destroyed by Predators No.	Destroyed by Predators %	Unknown No.	Unknown %	Total Number of Nesting Attempts
1967[a]	58	60	17	18	13	14	8	8	96
1968[a]	34	27	27	21	64	50	3	2	128
1969[a]	76	69	24	22	0	0	10	9	110
1970[b]	83	89	3	3	0	0	7	8	93
1971	75	78	13	14	2	2	7	7	97
1972	34	31	17	15	50	46	9	8	110
1973	82	71	21	18	6	5	7	6	116
1974[c]	78	90	3	4	1	1	4	5	86
Total	520	62	125	14	136	16	55	6	836

[a] Data from Ewaschuk (1970)

[b] Data from Westworth (1970)

[c] Nests were experimentally manipulated (see text)

Table 3. Fates of Canada goose nests on the small island in Dowling Lake. Data is not available for 1967, 1968 and 1970.

	Nest Fate						
	Successful		Abandoned		Destroyed by Predators		Total Number of Nests
Year	No.	%	No.	%	No.	%	
1969	3	100	0	0	0	0	3
1971	3	75	1	25	0	0	4
1972	8	89	1	11	0	0	9
1973	5	83	1	17	0	0	6
1974	3	100	0	0	0	0	3
Total	22	88	3	12	0	0	25

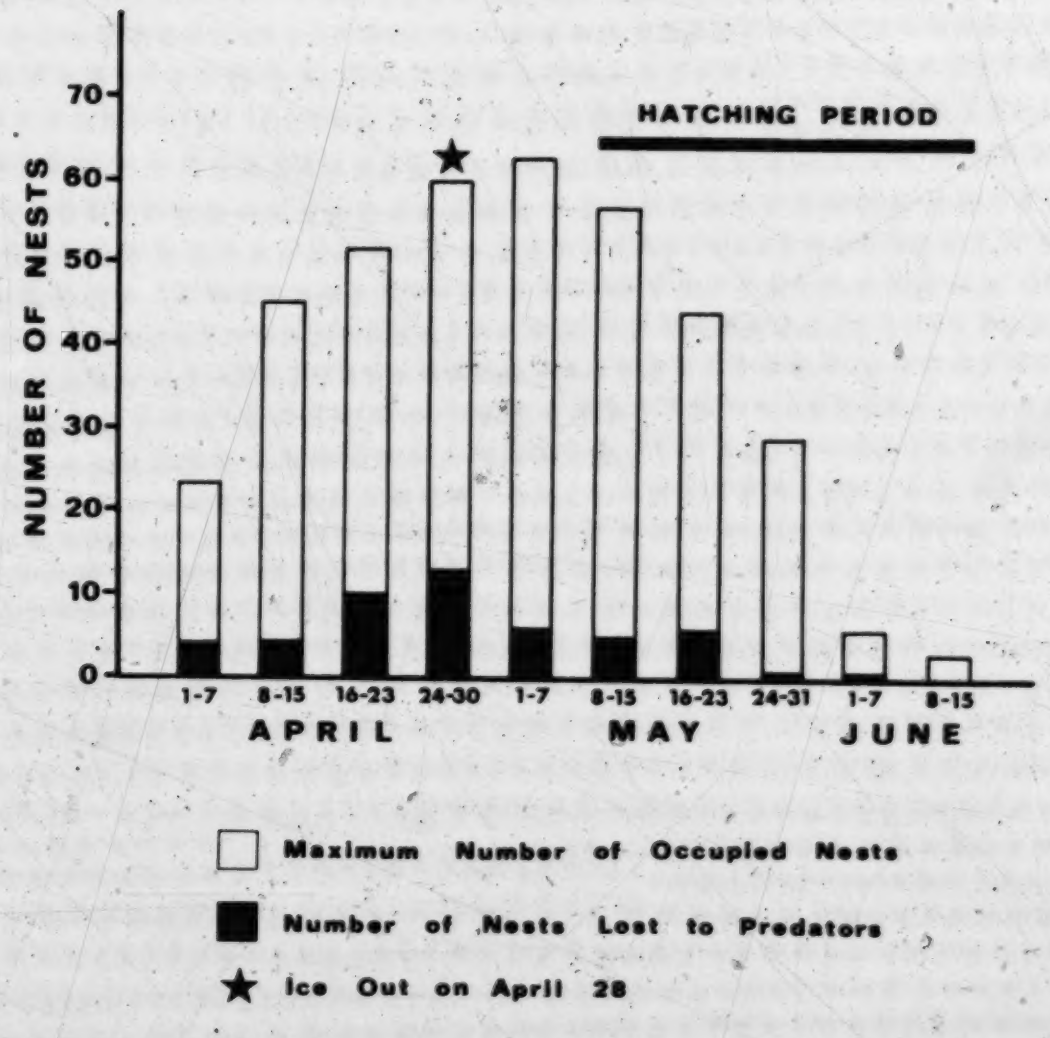
Table 4. Fates of Canada goose nests on the Spondin Lakes in 1972 and 1973.

Year	Nest Fate						Total Number of Nests
	Successful		Abandoned		Destroyed by Predators		
	No.	%	No.	%	No.	%	
1972	22	81	3	11	2	8	27
1973	8	44	2	12	8	44	18
Total	30	67	5	11	10	22	45

on her tail, was present on each occasion indicating that the same coyotes were likely responsible for most of the predation. Figure 9 indicates a drop in predation after the latter part of April. The difference between the proportions of nests lost to predation before late April and after approaches significance ($0.05<P<0.1$). The drop in predation occurred at the same time the ice disappeared between the island and mainland. Since the number of nests initiated was still increasing at this time, it seems likely that the reduction in predation was due to fewer coyote visits to the island, and the water barrier, although it did not stop coyotes crossing to the island, did act as a deterrent. Ryder (1967) found that arctic foxes (Alopex lagopus) gained access to the Ross' goose nests as long as an ice bridge remained between the mainland and the islands, but ceased to harass the geese once a definite water barrier was established. The coyotes were not a problem in years following 1972 when higher water levels prevailed at Dowling Lake and no ice bridge existed after the geese began to lay. Nest destruction by mammalian predators did not occur on the small island during this study. This island is several hundred meters from shore and was surrounded by water when nesting began in all years. Predators destroyed 10 of the 45 nests on the Spondin Lakes (Table 4) in 1972 and 1973. All ten losses resembled the pattern described by Rearden (1951) for coyotes. Losses were quite low in 1972 but drier weather in 1973 allowed easy overland access to many locations that had been secure islands when nesting commenced.

Avian predation, responsible for heavy losses of duck nests at Dowling Lake (Glasgow, unpublished data), was insignificant on goose nests. California gulls and crows (Corvus brachyrhynchos) scavenged fresh goose eggs during the laying period and unhatched eggs after incubation had ceased but were

Figure 9. Relationship between the numbers of occupied nests and the number of nests lost to predators on the large island in Dowling Lake in 1972.


NUMBER OF NESTS
0
10
20
30
40
50
60
70
HATCHING PERIOD
1-7
8-15
16-23
24-30
1-7
8-15
16-23
24-31
1-7
8-15
APRIL
MAY
JUNE
Maximum Number of Occupied Nests
Number of Nests Lost to Predators
Ice Out on April 28

known to destroy only two nests completely. Both nests were left partly uncovered while the pair was away on a feeding excursion. Nests on or near the gull colonies suffered the most frequent loss, and this was almost always during laying when many of the geese failed to cover their eggs while away from the nest. As described previously, California gulls destroyed one other goose nest while it was being abandoned. It appeared that covering the eggs with nesting material or down was an important factor in preventing avian predation. Some geese recognized the crows and gulls as potential predators and drove them away from the territory and/or the nest site, but other geese allowed gulls to establish nests less than 2 meters away from their own nests. The exact extent of the loss to avian predators is not known because they carry some eggs away from the nest site, but losses were probably less than 1 percent. Few interspecific interactions between the geese and gulls indicated that the gulls had evolved a respect for the geese since they did not usually attack exposed eggs or goslings even when left unattended, but readily preyed upon duck eggs and ducklings (Dwernychuk and Boag 1972a, 1972b; this study).

The percentage of successful nests on the large island in Dowling Lake was not significantly different between 1968 and 1972, but success in both these years was significantly lower than the other 6 years. There was no statistical difference between the other 6 years but production in 1967 was well below that for the other 5 years (Table 2). The reason for this is not known. As discussed previously, the marked reduction in success in 1968 and 1972 can be attributed to coyote predation. It should be noted that all nesting attempts destroyed by egg collecting in 1974 were not included in Table 2. Success was high on the small island during

all years (Table 3). Hatching success on the Spondin Lakes was high in 1972 but very reduced in 1973 through predation (Table 4).

The percentage of abandoned nests was significantly lower on the large island in 1970 and 1974 than in all the other years which were not different from each other. If the data for all 5 years for the small island are lumped, the percentage of abandoned nests was not significantly different from the lumped sample for the large island. Even though the geese on the Spondin Lakes nested at lower densities, there was no significant difference between desertion rates in this group and the Dowling Lake group. This suggests that the percentage of deserted nests may be fairly constant independent of density within certain limits, but data from 1970 and 1974 support Munro's (1960) suggestion that desertion rates were density dependent. Desertion rates may have been influenced by this study and other human disturbance but the impact is not known.

Ewaschuk and Boag (1972:Fig. 7, pp. 1105) suggest that the percentage of successful nests decreases with increasing numbers of nesting pairs. I think their study and this study in fact show this, but the numbers they used for "number of nesting pairs" may be misleading since these numbers represent numbers of nests initiated and not necessarily numbers of nesting pairs active at one time. I suspect that the higher number of nests initiated and the longer period of nest initiation in 1968 and 1972 may reflect many post-predation renesting attempts and not actual numbers of nesting pairs. However, natural renesting was not documented. The 1974 experiment showed that the potential for renesting is there and did occur when the nests were experimentally destroyed during or prior to the first week of incubation. The data from 1970 and 1974 strongly support the hypothesis that nesting success increases with decreased numbers of nesting attempts.

Figure 10 depicts the regression line as drawn by Ewaschuk and Boag (1972). This line remains unchanged with the addition of data from 1971-1974. However, if the years of high predation, 1968 and 1972, are removed, the slope of the line changes significantly (Fig. 10). I feel that this slope is probably more realistic as predation was not a factor in the other years. I also feel the number of nesting pairs was much more constant than the number of nest initiations would indicate. The extrapolated values for the regression line at 100 percent and zero percent success will likely never be reached as there are always unsuccessful nesters and the upper limits for density are restricted by territorial behavior. If existing nesting densities and average territory sizes of about 0.05 hectares represent minimum tolerable territory size, then the upper limit of about 100 pairs has already been reached on the large island in Dowling Lake unless the habitat is modified. If the smallest known territory (0.02 hectares) is used in the calculation, then the theoretical maximum number of pairs would be 250. Desertion rates may have been just as high on the Spondin Lakes because, even though nest densities are low, the competition for the few potential nest sites may be intense.

Productivity is determined both by the percentage of successful nests and the percentage of eggs that hatch in those nests. Table 5 indicates the mean clutch size, the percentage of eggs hatching from successful nests and the mean brood size expected as a result of the hatch from 1970 to 1974. There was no significant difference between years for any of these categories. The reason for the variability in the percentage of eggs hatching is not known but may be correlated with levels of disturbance; the year with the lowest hatching success (79 percent) was 1972, the year when disturbance from predators and observer visits was greatly

Figure 10. Relationship between the number of nesting attempts by Canada geese and their nesting success on the large island in Dowling Lake, 1967-1974. The coefficient of correlation (r) is -0.57 for the dotted line and -0.76 for the solid line.

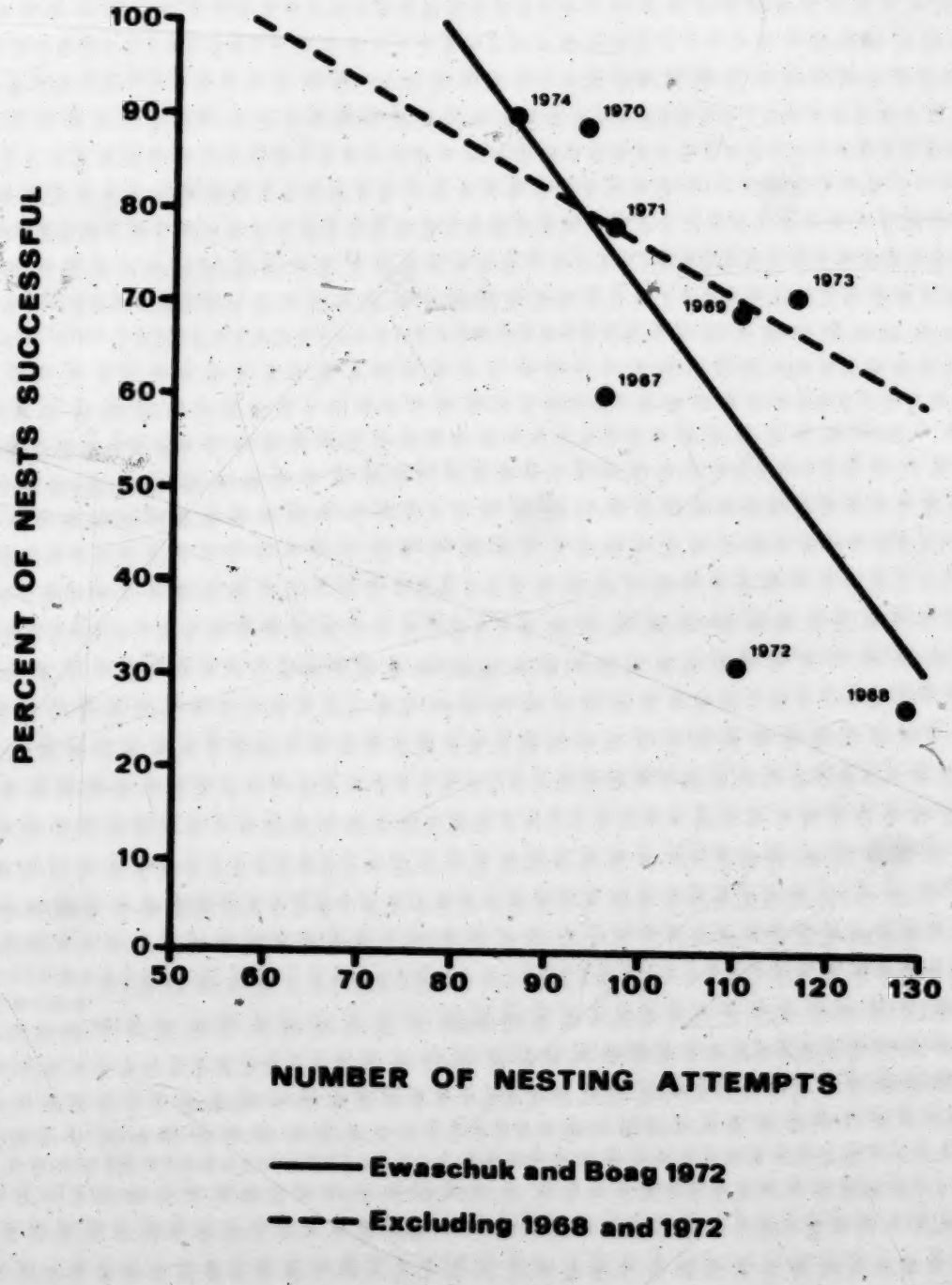

PERCENT OF NESTS SUCCESSFUL
100
90
80
70
60
50
40
30
20
10
0
50
60
70
80
90
100
110
120
130
1974
1970
1971
1973
1969
1967
1972
1968
NUMBER OF NESTING ATTEMPTS
Ewaschuk and Boag 1972
Excluding 1968 and 1972

Table 5. Percentage of eggs that hatched on the large island in Dowling Lake. The data were from successful nests only.

Year	Mean Clutch Size	Percentage of Eggs Hatching	Estimated Mean Brood Size at Hatching
1970[a]	5.3 (38)[b]	-	-
1971	5.6 (70)	89	5.0 (51)[b]
1972	5.2 (45)	79	4.1 (26)
1973	4.9 (83)	93	4.6 (73)
1974	4.8 (67)	95	4.7 (64)

[a] Data from Westworth (1970)

[b] Number of clutches used to determine the mean are in parentheses

increased. The percentage of eggs hatching in successful nests on the small island, where predation was absent and observer visits were fewer, was 85 in 1972. Hatching success in successful nests on the Spondin Lakes was 85 percent in 1972 and 1973. Five of 183 (2.7 percent) unhatched eggs were infertile and 178 (97.3 percent) had dead embryos in them. Most (86 percent) of the dead embryos were less than 5 days from hatching and probably died when the female left the nest with earlier-hatched goslings.

D. Platform Nesting, Associated Behavior and Hatching Success

It appeared that nesting was much denser in the willows where use of heron nests allowed Canada geese to establish both ground and tree nests very close together. Ewaschuk (pers. comm.) erected 40 wooden platforms on the large island at Dowling Lake in the fall of 1968 to see what effect use of these nest sites might have on adult behavior and territory size. These platforms are described in Appendix IIA. The 40 platforms remained in position as shown in Figure 3 until late summer 1973. Nine metal platforms (Appendix IIB) were placed in position over water (Fig. 11) in the fall of 1972. Twenty wooden platforms from the north (n) group and eight from the south (s) group were moved and placed over water in late summer 1973 as shown in Figure 11. High water levels and wave action destroyed 19 of the 39 wooden platforms and five of the nine metal drums were flooded before the 1974 nesting season began.

The use of nesting platforms on the large island in Dowling Lake during 1969 to 1974 is shown in Table 6. The number of platforms considered "available" were those which had sufficient material for nesting. "Tested" means that the platform was investigated as a potential nest site by paired geese. Some platforms were tested even though they had no nesting material in them. "Used" means that a nest was established and at least one egg was laid. Tree nests were those situated in the willows directly west of the large observation tower. All tree nests were more than 1 meter above the ground level.

The platforms were not used before 1971 with one exception. Westworth (pers. comm.) observed a gander sitting on one in 1970. Platform use in 1971 began on April 4 when a pair investigated 41s. Use built up slowly until 17 different platforms were being tested at one time. Thirty-three

Figure 11. Position of the 39 wooden and 9 metal nesting platforms in the fall of 1973.

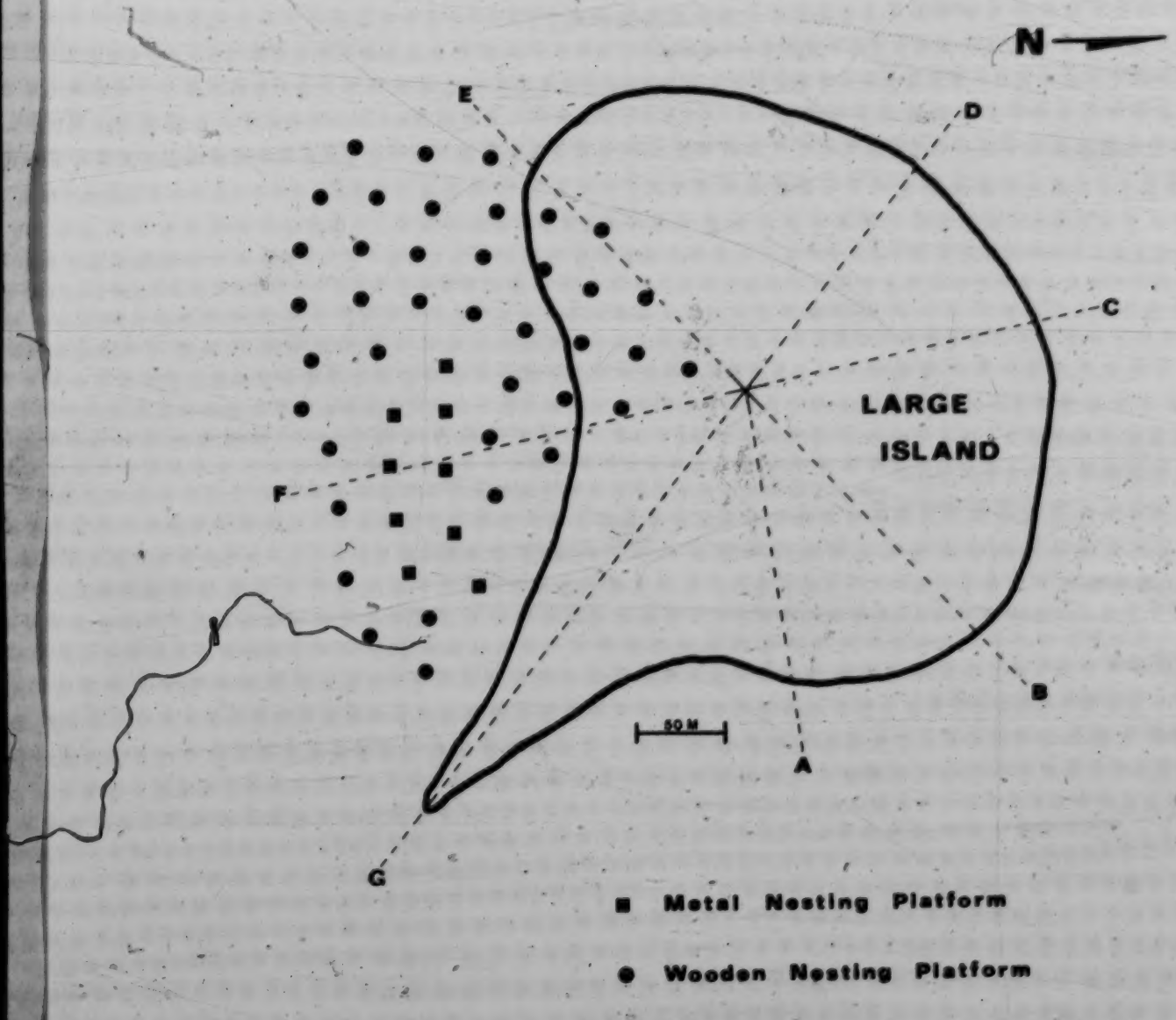

N
E
D
C
LARGE
ISLAND
F
B
50 M
A
G
Metal Nesting Platform
Wooden Nesting Platform

Table 6. Use of nesting platforms by Canada geese on the large island in Dowling Lake, 1969-1974.

Year	Number of Platforms						% of Available Platforms Used		
	Available		Tested		Used				
	Wood	Metal	Wood	Metal	Wood	Metal	Wood	Metal	Total
1969[a]	40		0		0		0		
1970[b]	40		1		0		0		
1971	23		33		8		35		
1972	31		40		12		39		
1973	33	7	39	9	6	2	18	29	20
1974	20	4	-	-	6	1	30	25	29
Total	187	11	113	9	32	3	17	27	18

[a] Data from Ewaschuk (pers. comm.)

[b] Data from Westworth (pers. comm.)

of the 40 platforms available were tested at least once (Table 6). The first nests initiated on the island in 1971 were in platforms 21s, 41s and 11n. Most of the ground on the island was snow covered at this time so this may have been the initial impetus for using the platforms. Nests were eventually established on eight platforms; four on the island (21s, 41s, 11n, 34n) and four over water (16s, 26s, 15s, 35s). The nests over water were established after peak nest initiation on the island and had a lower mean clutch size than those on the island suggesting that they were used probably by younger birds. An additional four nests were built directly below or within 1.5 meters of four platforms. Thirty-five percent of the available platforms were used by nesting pairs (Table 6), but non-breeding geese continued to test the platforms long after the last nest had been established. Use of embryo dyes (Appendix I) appeared to have prevented 100 percent hatching success in the platforms in 1971 (Table 7). Three of the four tree nests were successful while one was abandoned.

Platform use increased in 1972. Eight different platforms were tested on April 4 with a maximum of four at one time. Eventually all 40 platforms had been tested at least once with a maximum of 23 at one time. Nests were established in 12 platforms (nine on land, three over water) of which five were abandoned, four were destroyed by predators (three by coyotes and one by gulls) and three hatched successfully (Table 7). The poor success paralleled that for the rest of the nests on the island. The platforms were obviously not high enough to prevent access to coyotes, and the increased disturbances caused by the predators and observers probably caused the high rate of desertion. Two of the three successful nests were over water and were much more secure than those on the island.

Table 7. Hatching success of Canada geese using elevated nesting sites on the large island in Dowling Lake, 1969-1974.

Year	Number of Nests		Number of Clutches Hatching		Percent Nests Successful		
	Platform	Tree	Platform	Tree	Platform	Tree	Total
1969[a]	0	3	0	3	-	100	100
1970[b]	0	4	0	4	-	100	100
1971	8	4	8	3	100[c]	75	91
1972	12	2	3	2	25	100	36
1973	8	1	7	1	87	100	88
1974	7	1	6	1	85	100	87
Total	35	15	24	14	69	93	76

[a] Data from Ewaschuk (pers. comm.)

[b] Data from Westworth (pers. comm.)

[c] See text for qualifier

Both tree nests were successful. They were not higher than the platforms but were much better concealed. Thirty-nine percent of the available platforms had nests established in them in 1972 (Table 6); about the same as 1971 in spite of the increased useage in total numbers.

There was a decreased useage of platforms in 1973 (Table 6) even though the numbers of useable platforms increased substantially with the addition of nine new metal drums. All of the artificial sites were tested at least once during the nesting season but nests were established in only 20 percent (8 of 40) of the available platforms. Success was very high with only one clutch not hatching (Table 7).

Observations were not made in 1974 so the numbers of platforms tested is not known, but nests were established in 29 percent (7 of 24) of the available locations (Table 6). Hatching success was again very high with only one clutch lost (Table 7).

The steps that led to Canada geese using elevated nest sites are not known but learning appeared to be involved. During years of heavy snowfall, the snow packed into the willows so that old heron nests were only a few centimeters above the snow level even though they were 2-3 meters above the ground after the snow melted. Geese establishing nests early in the season used the snow-free heron nests and were able to walk right into them. Once having successfully used these nests, geese may have returned to them and similar sites again in subsequent years even though these nest sites were well above the snow and ground level at such times. Thus they learned to use or became habituated to an elevated nesting situation. Elevated tree nesters were present throughout this study and historically may have produced birds imprinted to an elevated site after having hatched there. It is possible that some of these birds began the

initial platform testing in 1971, but the numbers of geese testing the platforms subsequent to this could only be explained by a learned response in the flock. Contagious behavior, where an action by one bird causes the same action in another bird, is very common in Canada geese, and likely contributed to the rapid response to the platforms once they had been tested a few times. However, the ground nesting tradition also remained strong and platform use never exceeded 40 percent of those available.

The original hypothesis was that use of platforms would decrease territory size and allow more geese to nest on the island. To test this, I lumped the samples for 1971-1974 to increase the sample size. Comparing the mean nearest-nest distance for platform nests (18.3 meters) with that for ground nests (16.9 meters) gave no significant difference. Only platforms located in the vegetated part of the island were considered since those over water could not be closer to the next nest than 30.5 meters due to the spacing of the platforms. Since the nearest-nest distances suggest that territories around land based platforms were similar in size and shape to those of ground nesting pairs in the same area, the hypothesis can be rejected.

Behavioral differences between platform nesters and ground nesters were noted in 1971, the only year during which observations were made. Ganders with ground nesting females spent less than 1 percent of their time within 2 meters of the nest site, but ganders with platform nests spent from 18 to 38 percent of their time on the platform deck. Time spent by ganders at the nests in over-water platforms was not significantly different from that at over-land platforms. The increased time that ganders spend on the platforms may be necessary to deter attacks on the female by

neighboring ganders. Females on platforms appeared to be more visible to adjacent geese than ground nesters. All ganders defending platforms also had some ground based territory, even those using platforms over water. Ganders from over-water platforms spent time away from the nest in the water around the platform or on the adjacent shore of the island. The shore areas were defended only while the gander or the female were loafing there, but no attempt was made to defend them if both geese were at the nest site. The water around the platform was defended just like a territory around a land-based nest. There were no other obvious behavioral differences between platform nesting and ground nesting geese.

Hatching success for Canada geese using elevated nest sites on the large island in Dowling Lake is summarized in Table 7. Hatching success was consistently higher in elevated nests than in ground nests but the difference was not statistically significant (G-test, Sokal and Rohlf 1969).

The overall impact of the platforms on the reproductive output of Canada geese at Dowling Lake was very small. If the platforms could be successfully placed farther off the island, the breeding population and productivity might increase, but it seemed evident that the nesting density on the island was at or approaching the maximum for this population of geese, with or without platforms.

E. Post-hatch Brood Behavior and Survival

Brood Movements, Dispersal and Distribution

Goslings and parents left the nest about 1 day after hatching. No broods were known to return to the nest site for brooding as Collias and Jahn (1959) observed, but one female did return to her nest with 4 goslings (after a short feeding-bathing foray of 63 minutes) for 1 day and successfully hatched a fifth egg. Broods often went directly to the water and moved off the large and small islands in Dowling Lake to the mainland, but some broods remained on the island for several days. All broods eventually moved to the mainland and exhibited extensive movements around and/or off Dowling Lake.

Many broods returned to the island at night, but others remained on the mainland; at least until dark when last observed. Thirty-four percent of all broods observed (106 brood observations on 12 days between May 10 and June 23, 1973) at least once on the mainland shore at some time during the day were known to have returned to the large island by the time observations ceased at dusk. Whether the broods remained on the island all night and whether more birds moved there after dark are not known. This represents only birds seen from the two observation towers on the large island (a maximum of 27 percent of the broods on the lake were seen on any one observation day) and not those dispersed elsewhere on the lake. The islands provided a secure brooding site free from mammalian predation. Marked adults indicated that the same broods were not involved in this movement every day. Observations of this type were only noted until the goslings were about 5-6 weeks old so it is not known if older broods show the same tendencies for secure night roosting on the islands.

Brood movements varied among broods and from day to day. Broods often moved less than 100 meters during an entire day if they were not disturbed but moved several kilometers on other days. Figure 12 gives sighting locations for two broods on sequential observation days to give some indication of their movement. Movements on and around the lake were more frequent on calm, sunny days than windy, cool, cloudy days. Mobility increased as the goslings became older.

There was a definite dispersal from the breeding islands on Dowling Lake to water bodies off the lake. This was quite distinct from occasional forays by some broods off the lake to adjacent ponds as they subsequently returned to the lake. Dispersal was assumed if the brood was observed on the same water body for more than 2 weeks. Figure 13 shows the destination of dispersing broods hatched on Dowling Lake in 1972 and 1973. Eight broods (19 percent of those produced) moved off Dowling Lake in 1972 and 22 (25 percent of those produced) in 1973. It is not known whether the same adults were involved in both years. Perhaps some of these adults had been raised in these same ponds. Dispersal in all cases occurred when the brood was less than 2 weeks old. The actual route of dispersal is unknown but movement of several hundred meters overland was required to reach some of the water bodies (Fig. 13). The numbers of broods dispersing to the various lakes are indicated in Figure 13. All the broods remained on these areas off the lake for the entire observation period with one exception. In 1972 the broods on lake K were harassed during banding and subsequently returned to Dowling Lake. In 1973 six broods moved from lake P to lake S after having been on P for about 5 weeks and one brood moved from lake O to P after having been there for 8 days. Lakes A, D, E, J, M, N and U were all used during the brood

Figure 12. Sequential sightings of two Canada goose broods on Dowling Lake in 1973.

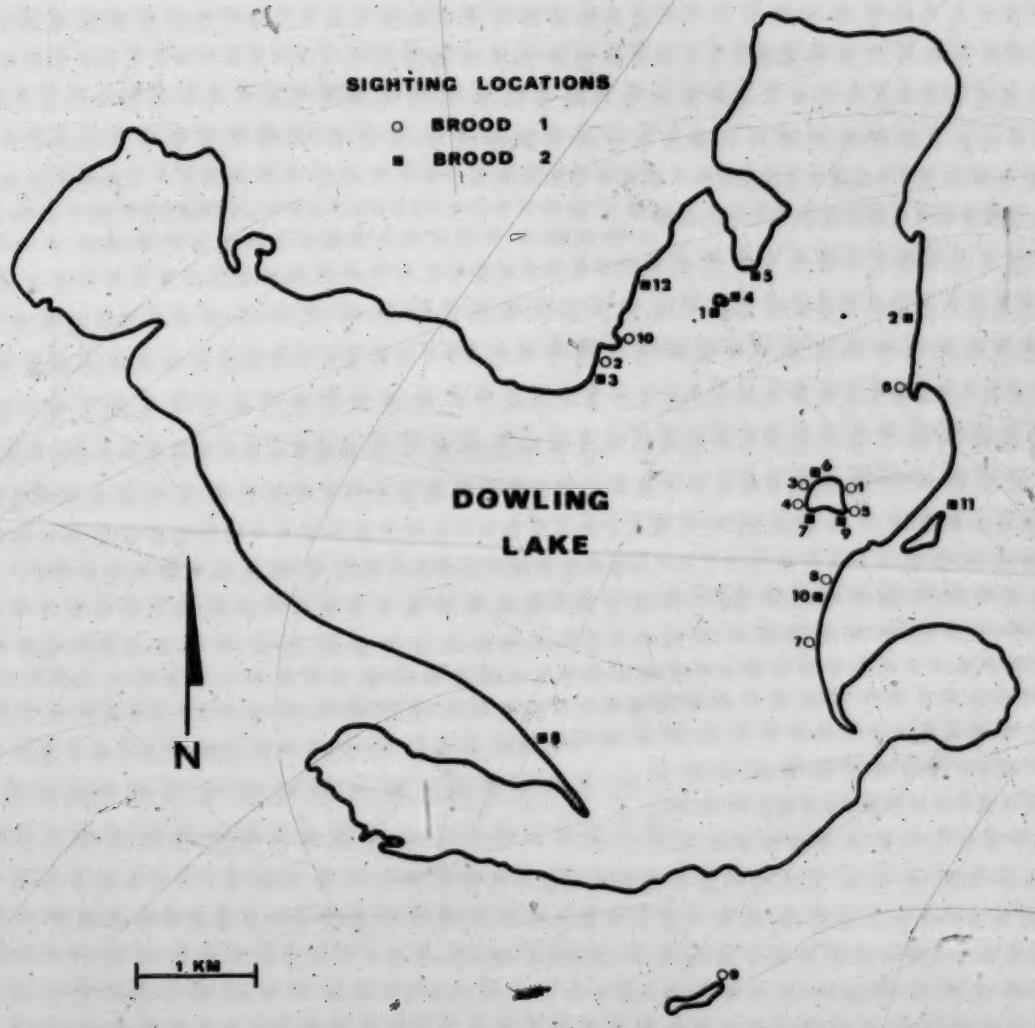

SIGHTING LOCATIONS
BROOD 1
BROOD 2
DOWLING
LAKE
N
1 KM

Figure 13. Locations to which broods of Canada geese, hatched at Dowling Lake, dispersed during the summers of 1972 and 1973. Numbers of broods dispersing are indicated at the base of the arrows.

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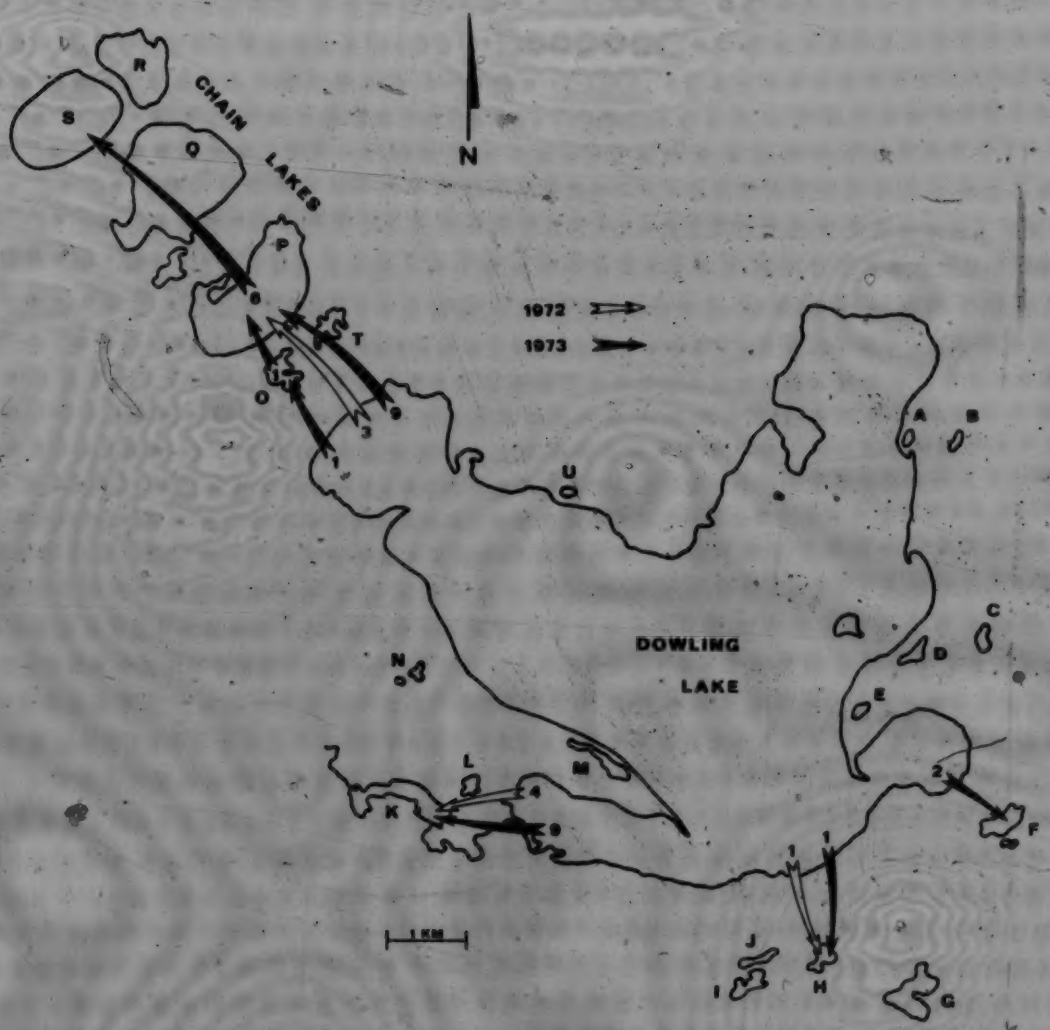
CHAIN LAKES
DOWLING LAKE
N
1972
1973
1 KM
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U

rearing period but no broods remained there for any great length of time. For purposes of discussion they are assumed to be part of the associated shoreline unit.

The distribution of broods on Dowling Lake was recorded on 22 days in 1972 and 20 days in 1973 to give an indication of the spatial use of the shoreline. Figure 14 shows the shoreline units. These equal linear units are numbered 1 to 106 and are about 400 meters long. Broods spent the majority of their time within 100 meters of the water so the units are linear rather than a certain area. The large and small island were arbitrarily assigned shoreline unit numbers 107 and 108. All units were observed an equal number of times.

Table 8 indicates the number of brood observations within each shoreline unit over the total observation period (i.e. one brood could be tabulated more than once). It is obvious that the broods were using only a small percentage of the potential brooding area in both 1972 and 1973. Five areas were heavily used in both years. These were the large and small islands, the shoreline adjacent to the large island (units 5-8), the shoreline near the small island (units 77-81) and shoreline units 101-102. Comparison of plant communities between heavily used and unused shoreline locations indicated very little difference. Most of the observations indicate an affinity for the breeding islands or the adjacent shore. This may just be a function of being more familiar with the shore area near or on the nesting islands, or it may be a selected behavioral mechanism for brood survival. Obviously, those broods near or on the islands have rapid, easy access to a secure brooding location day or night. There was a marked increase in brood use of the islands after the adults had molted their flight feathers. This supports the hypothesis that a site free from

Figure 14. Shoreline units on Dowling Lake.

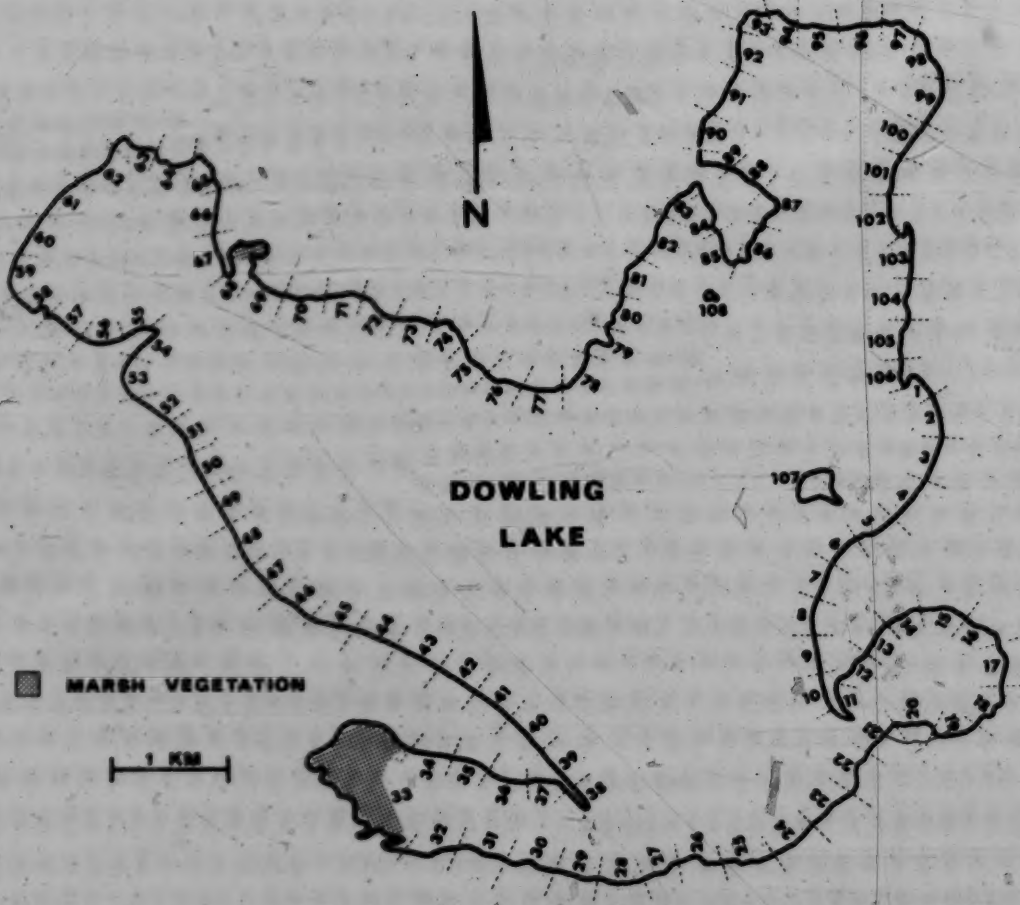
N
DOWLING
LAKE
MARSH VEGETATION
1 KM

Table 8. Numbers of brood observations of Canada geese within each shoreline unit on Dowling Lake in 1972 and 1973.

Shoreline Unit	No. of Observ.		% of Observ.		Shoreline Unit	No. of Observ.		% of Observ.	
	1972	1973	1972	1973		1972	1973	1972	1973
1	6	0	2.9	0	41	0	3	0	1.4
2	2	0	1.0	0	42	0	0	0	0
3	0	0	0	0	43	0	0	0	0
4	0	2	0	1.0	44	1	0	0.5	0
5	5	13	2.4	6.3	45	1	0	0.5	0
6	11	40	5.3	19.2	46	2	0	1.0	0
7	12	31	3.8	14.9	47	1	0	0.5	0
8	8	11	3.9	5.3	48	0	0	0	0
9	0	0	0	0	49	1	0	0.5	0
10	0	0	0	0	50	0	0	0	0
11	0	0	0	0	51	0	0	0	0
12	0	0	0	0	52	0	0	0	0
13	0	0	0	0	53	0	0	0	0
14	0	0	0	0	54	1	0	0.5	0
15	0	0	0	0	55	2	0	1.0	0
16	0	0	0	0	56	0	0	0	0
17	0	0	0	0	57	0	0	0	0
18	0	0	0	0	58	0	0	0	0
19	0	0	0	0	59	0	0	0	0
20	0	0	0	0	60	0	0	0	0
21	0	0	0	0	61	0	0	0	0
22	0	0	0	0	62	0	0	0	0
23	0	0	0	0	63	0	0	0	0
24	0	0	0	0	64	0	0	0	0
25	0	0	0	0	65	3	0	1.5	0
26	0	0	0	0	66	5	0	2.4	0
27	1	4	0.5	1.9	67	0	0	0	0
28	0	0	0	0	68	8	1	3.9	0.5
29	0	0	0	0	69	2	0	1.0	0
30	0	0	0	0	70	1	0	0.5	0
31	0	0	0	0	71	3	0	1.5	0
32	0	0	0	0	72	5	0	2.4	0
33	0	0	0	0	73	1	1	0.5	0.5
34	0	0	0	0	74	0	0	0	0
35	0	0	0	0	75	1	0	0.5	0
36	0	0	0	0	76	3	0	1.5	0
37	0	0	0	0	77	6	0	2.9	0
38	0	0	0	0	78	7	0	3.4	0
39	0	1	0	0.5	79	22	8	10.7	3.8
40	1	0	0.5	0	80	13	3	6.3	1.4

... continued

Table 8. Continued

Shore-line Unit	No. of Observ.		% of Observ.	
	1972	1973	1972	1973
81	2	3	1.0	1.4
82	1	0	0.5	0
83	1	0	0.5	0
84	2	0	1.0	0
85	1	0	0.5	0
86	0	0	0	0
87	0	0	0	0
88	1	0	0.5	0
89	1	0	0.5	0
90	0	0	0	0
91	0	0	0	0
92	0	0	0	0
93	0	0	0	0
94	0	0	0	0
95	1	0	0.5	0
96	0	0	0	0
97	0	0	0	0
98	0	0	0	0
99	0	0	0	0
100	0	0	0	0
101	6	15	2.9	7.2
102	3	0	1.5	0
103	2	0	1.0	0
104	0	0	0	0
105	0	0	0	0
106	0	0	0	0
107	40	66	19.4	31.7
108	10	6	4.9	2.9
TOTAL	206	208	100.5	99.99

mammalian predators was the preferred brooding location. There is no known explanation for heavier use of the 101-102 shoreline units which were not close to the islands and did not provide secure roosting sites. There was no correlation between mainland feeding sites used by adults during nesting and subsequent dispersal or use of brooding sites by the same adults. The use of very small parts of the potential area for brood rearing had important implications for brood mixing.

When broods were observed in the shoreline units, the distance to the nearest brood was recorded. The purpose of this was to see whether broods were solitary or tended to aggregate. Table 9 shows the tendency toward brood aggregation at Dowling Lake in 1972 and 1973. The numbers represent all brood sightings on the sampling days so any individual brood could be included several times. Thirty meters was arbitrarily chosen because broods this close together are within the range of potential interaction with their neighbors. Broods were observed in aggregates 78 percent of the time in 1972 and 75 percent in 1973 (Table 9). Groups of 2 to 4 broods were the most common in both years. Broods also spent a lot of time alone, 23 percent in 1972 and 25 percent in 1973. Thus broods showed a significantly clumped distribution on any one sampling day. Although some of the aggregates likely just represented mutual use of an area, marked birds revealed that some brood associations consisted of the same individual broods on consecutive days regardless of the area they were in at the time. Three groups in 1972 and 4 in 1973 were seen together on more than 70 percent of the observation days, but no aggregates were known to remain stable during the entire observation period. As the broods matured, aggregation became more evident. Just prior to fledging there were three large groups in 1971, two in 1972 and

Table 9. Tendency toward brood aggregation at Dowling Lake in 1972 and 1973. Broods were considered an aggregate if two or more were within 30 meters of one another. The term "brood" means sibling brood or mixed brood.

	No. of Observations		No. of Broods Represented		Percent of Broods Represented	
	1972	1973	1972	1973	1972	1973
Single Broods	77	70	77	70	23	25
Aggregates						
2	26	55	52	110	16	39
3	21	23	63	69	19	22
4	28	7	112	28	34	10
5	3	1	15	5	5	2
6	1	1	6	6	2	2
7	1	0	7	0	2	0
Subtotal	80	87	255	212	78	75
Totals	157	157	332	282	100	100

three in 1973. These groups may fly as independent flocks in the fall, but this could not be substantiated because observations were discontinued before flight was attained.

Brood Mixing Behavior

The three factors that set the stage for brood mixing to occur have already been discussed. These were synchronous hatching, use of a relatively small area for brood rearing and the tendency for broods to aggregate. These three factors facilitated the many interbrood contacts that were necessary for brood mixing to occur. Seven individual brood takeovers were observed in 1972 and 1973. These will be detailed to illustrate the mechanism of takeover and describe the behavior of the adults involved. The pair taking over the goslings will be known as the "recipient" pair or brood and the pair losing its goslings will be known as the "donor" pair or brood. All goslings were Class Ia (Southwick 1953 and Yocum and Harris 1965) unless otherwise specified.

Takeover 1 (May 23, 1972): Two broods were first observed about 20 meters apart on shoreline unit 4 at 2027 hours (Mountain Daylight Time - MDT). The donor brood of three goslings moved toward the recipient brood of seven goslings at 2032. When the donor pair was about 3 meters away, the gander of the recipient brood attacked and chased the donor brood adults about 100 meters away. The three donor goslings mixed with the recipient brood. The gander of the recipient pair returned to the brood while the donor pair, calling constantly, approached within about 25 meters of the mixed brood. Intensive threats by the recipient gander kept them from moving closer. The donor goslings showed no signs of returning to their parents despite repeated calling by their parents.

The mixed brood continued to feed and rest in this vicinity until dusk, about 2133,when the female started brooding the goslings. During this time the donor pair remained about 25 meters away. The mixed brood of ten goslings was seen the following day but there was no sign of the donor pair. Goslings of both pairs were about 3 days old. The donor female was a known adult (3+ years) that had raised a brood the previous year. The status of the other adults was not known.

Takeover 2 (May 14, 1973): A brood of five goslings was feeding on shoreline unit 5 at 1330 hours (MDT). A brood of four goslings swam to the shore in unit 6 at 1345 about 200 meters away while a third brood of one gosling was swimming in the water between them. The brood of five entered the water at 1354 and swam towards the broods of four and one (now only 25 meters apart on the shore). At 1404 the broods of five and one were only 20 meters apart on the shore while the brood of four moved off toward shoreline unit 7. The brood of one moved toward the brood of five at 1455 followed by both broods entering the water and moving toward one another. Swimming very slowly these two broods finally came within 5 meters of one another at 1523. There was much head posturing with high intensity threats by the adults as the goslings mixed. When the pair with five goslings moved off, all six goslings went with them and the donor pair followed about 10 meters behind, continuing to threaten. All went ashore. The donors preened for 2 minutes and then walked slowly about the recipient pair with low neck coil threats (1525) while the recipient brood rested on the shore. At 1528 the donor female was preening, the donor male was standing erect and the mixed brood was feeding. A brood of 12 goslings swam by about 30 meters away and the donor male threatened them with head flips and a low neck coil approach. Afterwards at 1532 the donor pair

flew out into the water and was feeding and preening there. They returned to shoreline unit 6 at 1542 and continued to rest and feed there until 1700 when they swam out towards the middle of the lake. No attempt was made by the donors to regain their single gosling after the initial try, and they did not follow the recipient brood when they left the area at 1543 hours. Both the donor and recipient goslings were less than 5 days old. The status (age, sex) of the four adults involved was not known.

Takeover 3 (May 16, 1973): A brood of 18 goslings was first seen on the southwest point of the large island at 1515 (MDT). A newly hatched brood of three goslings appeared at 1533. The male of the brood of three rushed and chased three subadult geese on the shore and in so doing brought his brood within 5 meters of the brood of 18 (1541). The three newly hatched goslings moved over to join the larger group of 18. There was a great deal of head posturing and flipping, feather shaking, low neck coil threats and calling by both the donor and recipient ganders but no attacks. The donors moved off slowly and began preening and bathing at 1607, and subsequently swam around the point out of sight at 1636 and did not return. There were 23 individual fights noted between the 18 recipient goslings and the three donor goslings but by 1820 these were occurring infrequently as the brood moved across to shoreline units 6 and 7. They were still there at dark (about 2145). The brood of 18 had obviously been involved in brood mixing previously but there were still no goslings older than 5 to 7 days. Status of the adults was not known.

Takeover 4 (May 16, 1973): A brood of four goslings (about 7 days old) was first seen at 1734 (MDT) just north of the large observation tower on the large island. A brood of three goslings (not more than 2 days old) appeared from around the north end of the island and was swimming

toward the tower (1746). The donor brood of three came onshore about 15 meters from the recipient brood of four which had been feeding. There were mild threats exchanged and both broods began feeding with three moving toward four. At 1806 one of the three goslings moved across to join the brood of four followed by intensive threat postures by both adult males. The remaining two donor goslings joined the recipient brood at 1809 with both pairs continuing to posture. All seven goslings remained with the recipient pair and continued feeding while the donor pair continued to posture about 10 meters away. The recipient brood, now a mixed brood of seven, moved south past the tower and over to the mainland (shoreline unit 5) at 1822. They returned to the southwest point of the island at 2116. The donor pair remained in the area north of the tower for the rest of the day feeding, preening and resting. Status of the adults was not known.

Takeover 5 (May 18, 1973): The donor brood of three was first seen near the tall willows north of the large observation tower on the large island (Fig. 7) at 1410. The brood was newly hatched and moved slowly toward the shore of the island. A pair (Yellow GI gander) with eight goslings (about 10 to 12 days old) and a third brood of seven were feeding north of the observation tower spaced about 30 meters apart. The newly hatched brood arrived at the shore between the other two broods at 1520. There were mild threat postures by all three pairs. The brood of seven moved slowly toward the brood of eight and pushed the brood of three toward them also until all three broods were only 5 meters apart. There was an increase in intensity of threats by all three ganders. The donor goslings were moving slowly toward the brood of eight while their parents remained stationary. At 1526 the goslings moved to join the brood of eight.

One of the donor goslings returned to his parents for 14 seconds but then returned to the larger brood. The recipient brood, now 11, moved around the island out of sight at 1529 with the gander leading. The donor pair was following about 5 meters behind in the low neck coil threat posture. Neither the donor nor recipient pair were seen again that day, but the recipient brood was observed again in subsequent days with 11 goslings. The gander (GI) was banded as an adult in 1971 and had likely raised a brood that year. He was not successful in raising a brood in 1972 because the nest was lost to predation. Status of the other adults was not known.

Takeover 6 (May 24, 1973): The largest brood seen on May 18 was 11 but on May 22 two broods of 30 and 25-30 were seen. Subsequently on May 24 a large brood of 53 was seen with three adults (two females and one male). The goslings in the brood ranged in age from about 6 to 20 days. This brood arrived on the shore of the large island at 1934 on May 24. Several other broods were feeding in the same general area on the island. Another brood of six (about 4 days old) appeared at 2053 between the large brood of 53 and a brood of 10. All three broods were quietly feeding as the brood of six slowly moved toward 53. They came within about 10 meters before the gander showed any threat postures. The adults of the donor pair stopped moving, but the goslings continued to move and joined the large brood at 2104. The donor pair showed vigorous threat postures for 3 minutes, but at 2107 after preening and bathing on the shore, they swam away from the island and out of sight. The large brood remained on the island. Within a few days only one male and one female accompanied the large brood. Status of the adults involved in this takeover was not known.

Takeover 7 (May 24, 1973): A brood of 10 (about 12 days old) and a brood of three (about 4 to 5 days old) were feeding on the southwest

point of the large island at 1432. The broods, about 35 meters apart, were slowly moving together. The males began to posture vigorously at 1446 when the broods were only 10 meters apart. Goslings of both pairs continued to feed as they moved closer together. At 1453 the three donor goslings moved about 4 meters to join the recipient brood of 10. The donor pair continued to posture and follow the mixed brood of 13 around the point as they went out of sight at 1507. There were six fights between the donor and recipient goslings during the time they were in view. The status of the four adults was not known.

Although only seven individual takeovers were observed, a number of common themes emerge. Clearcut dominance of the donor adults by the recipient adults was noted in only one of the seven takeovers. In the other six cases there appeared to be a standoff with regard to dominance. The donor broods all had fewer goslings than the recipient broods. Donor goslings were always less than 5 days old, but the recipient broods had goslings ranging from about 3 days to 20 days in age. The recipient adult geese did not appear to be actively recruiting more goslings. In one case they were likely defending the area around their own brood and, in chasing the donor adults away, allowed the donor goslings to join their own brood. In the other six cases it was obviously the goslings that were responsible for the brood mixing. It appeared that young goslings, less than 5 or 6 days old, were more attracted to other goslings, especially if they were in groups larger than their own brood, than their own parents. The goslings showed very strong "follow the leader" tendencies similar to that described in ducks by Collias and Collias (1956) and Williams (1974). In all cases observed, the entire brood was involved in the takeover. It was also obvious that they did not respond to repeated calls by their

parents and seemingly did not recognize them either through visual or auditory cues although one gosling returned to its parents momentarily. Fabricius (1964) identified a very short critical period during which the following response can be elicited after hatching but suggested further refinement could take place for a longer period of time. During this study the goslings imprinted on and followed Canada geese but were not able to distinguish individual geese until about 5 days of age. Cowan (1973) showed that goslings exhibit some recognition of individual adult Canada goose calls and could distinguish them from gull calls. Beer (1970) reviews the individual recognition of voice and its importance in several other species, especially in situations where nesting is colonial and the young are mobile. It seems that although goslings learn quickly to follow adult geese, it takes a few days to refine individual auditory and visual recognition of their parents. Goslings older than 5 or 6 days often intermingled on the feeding areas but could recognize their own parents and readily sorted themselves out when the broods moved apart.

The donor adults appeared to lose their broodiness in the absence of their goslings and in most cases made little attempt to get them back. The fact that they did not attack the recipient pair in an attempt to get their goslings back may be an indication that they were lower in dominance but this is unknown. They very quickly turned to maintenance or perhaps displacement functions such as preening, bathing and feeding and the one marked female had joined a small group of unsuccessful nesters and non-breeders the next day. It seems likely that other donor pairs joined groups of unsuccessful nesters and non-breeders as well.

Another type of brood mixing might occur when goslings stray from their parents or their parents are killed. These goslings could then join the

broods of other pairs of geese. This may have happened at Dowling Lake but was not observed during this study. Acceptance of strange goslings by adult geese with broods was not always the rule. Two cases were observed in which single stray goslings about 5 days old were prevented from joining Class Ia broods with six and seven goslings respectively. The adult geese in both cases pecked at the intruder driving it off in one instance and inflicting head wounds leading to death in the other.

The experimental introduction of goslings from the hatchery in 1974 was attempted for two reasons. Although goslings less than 5 days old would seem ideal because they would probably mix readily with resident broods, they are difficult to catch and handle in the field at this age. Therefore, the experiment tested whether or not older goslings, 9 to 15 days, would mix with and be accepted by resident broods. Goslings older than 5 days were not observed mixing at Dowling Lake. Thus, this experiment tested age and filial bonds as factors influencing brood mixing in Canada geese.

Seventy-four goslings, ranging in age from 9 to 15 days old, were placed in holding pens on the large island in Dowling Lake on May 20, 1974. Territorial California gulls killed 12 goslings in the holding pens during the first 2 hours so the rest of the goslings were released. After 5 hours of observation, there were still 62 goslings alive and they were split into groups of 3, 5, 7 and 47. No contact had been made with any of the resident broods. Observations were not made again until the banding drive on July 1, 1974 when 56 of the 62 were trapped. Thirty-six were marked with individual neck collars. Thirty-three of these were seen during the July 28, 1974 brood survey and were arranged as follows: 2 in a brood of 27, 14 in a brood of 17, 4 in a brood of 8, 2 in a brood of 4, 3 in a brood of 5,

3 in a brood of 6 and 5 in a brood of 11. Brood here means only the goslings but all were accompanied by two adults. This indicates that the large group of goslings released had split into many smaller groups that were accepted by resident broods on the lake. Thus goslings 9 to 15 days of age are suitable for transplanting.

Although goslings at Dowling did not mix when they were older than 5 days, the hatchery reared goslings did, suggesting that age alone was not the critical factor. I suspect filial bonds were very important. In order to test this matter further, parentally exposed and parentally naive goslings of different ages would have to be introduced into similar situations. Both resident and introduced geese should be tested from several different genetic stocks to see if innate behavior or genetic predisposition for mixing are influencing their behavior, or if it is simply a function of density.

Brood mixing is mentioned frequently in literature concerning many populations of Branta canadensis maxima and Branta canadensis moffitti, but is has seldom been described in detail. Collias and Jahn (1959:496-497) said:

> "Adoptions of strange goslings were most likely to occur when both their own and strange goslings were less than one week old, and of about the same size. These younger goslings have apparently not yet become thoroughly acquainted and attached to a specific parent bird, nor their parents to them. Adoption is also facilitated by dominance of the foster parents. When a gosling accidentally gets into another brood and is allowed to remain with that brood, its parents may be thwarted in their endeavors to get it back, by the aggressive attacks of the other parents defending the vicinity of their own brood. Adoptions were rare in the case of goslings more than one week of age. Relatively permanent adoptions were common in the somewhat crowded conditions prevailing within the breeding pen, and three pairs of birds lost their entire broods through adoption by other parents."

They were working with a semi-captive flock but their observations basically agree with those of this study. There is some suggestion that the donor pairs may have attempted to get their goslings back which was not the case in my study. They were also working in a situation where the broods were forced together rather than associating by choice. They also suggested that the dominance of the foster parents was important. This was not obvious at Dowling Lake.

Sherwood (1966:243-244), studying Branta canadensis maxima in Michigan, found:

> "Brood mixing was common at Seney. It was common for the first two to three weeks of the goslings' lives and in some cases, continued into the fourth week. The largest mixed brood contained 23 goslings. The mixing phenomena were brought about by the natural gregariousness and because neither the parents nor the goslings could recognize one another. The parent geese developed the ability to recognize their 'own' goslings in 2-3 weeks time, but the goslings could not recognize their 'parents' or 'broodmates' until 5-6 weeks of age. Dominance and brood size were the most important factors in the buildup of a large, mixed brood. Pairs in which the adult female was a two-year-old usually lost their entire brood through the mixing process."

Sherwood (1967:354) also stated that the, "2-year-old females were most vulnerable in losing their goslings to older, aggressive pairs." This is quite different from the Dowling Lake situation where goslings and parents seemingly recognized each other at about 1 week of age. Fighting between recipient and donor goslings at Dowling suggests that they did recognize "broodmates". Dominance did not appear important at Dowling but brood size did. Larger broods appeared to attract potential donor goslings to join them more readily than smaller broods.

There were not enough marked adults at Dowling to determine the importance of adult age in brood mixing, but it seems likely that older, more experienced birds might nest earlier as suggested by Geis (1956) and Brakhage

(1965). They also showed clutch size increased with the age of the female. Hanson (1953) and Raveling (1967) said that the size of the brood affected the dominance; larger broods being more dominant. Balham (1954) suggested that the physical size of the goslings was important; families with older goslings were dominant over those with younger goslings. This may be partly a function of younger families showing more caution and avoidance of all other geese. If age of the breeding female was correlated with timing and brood size at Dowling Lake, then it would follow that older birds were the recipients in most of the brood mixing. Age of the females was not known but larger broods were the recipients in all cases observed. It then follows that once a mixed brood is established, it would attract more and more goslings resulting in a few large mixed broods rather than many small ones. Two-year-old females were not the major donors at Dowling because they constituted only 10 percent of the breeding females during the years of this study, and of this 10 percent about 20 percent were successful in raising their own broods. No known 2-year-old females were recipients during brood mixing. Although it is still possible that most of the donor broods were from younger, less experienced females (2, 3 and 4 years of age), there were five donor females in 1972 and 1973 known to have raised a brood successfully the previous season. This suggests that they were not always losers and that losing broods may be largely a matter of chance.

Balham (1954) said that the female leads the brood during the first 3 weeks. Since the first week is the critical time when other broods must be avoided to prevent brood mixing, the relative importance of the dominance status and experience of the male is not known. He is still the major defender if the female leads the brood into contact with another

brood.

Brakhage (1965:767-768), working with B. c. maxima in Missouri, describes a different type of brood mixing as follows:

> "It ordinarily started after the goslings were 5-7 days old. Creches were accompanied by two to five productive pairs and a variable number of non-breeding females. The pairs involved in gang brooding varied from year to year, but those hatching goslings first were most likely to become escorts. Pairs which started a creche remained in attendance throughout the brood-rearing period. Pairs which gave up their broods to a creche usually returned to the vicinity of their nesting territories. Some pairs appeared to approach social equality and, possibly as a matter of convenience, accepted each other as fellow escorts. The size of creches varied, but the largest recorded contained 110 goslings accompanied by 21 adults and subadult geese."

This is different than that described by most authors. All known broods at Dowling Lake that were older than 1 week maintained their integrity even when they did mingle, and there was a gradual increase in flocking together of broods with increasing age of the goslings. One situation comparable to that described by Brakhage occurred when two large broods came together and most of the goslings in both broods were greater than 5 days old. This very large brood of 59 goslings was accompanied by four adult geese for a few days, then three adults and finally only one pair. Both pairs appeared compatible during the short period they were together. Why the two adults eventually disappeared is not known.

Behavior of Sibling and Mixed Broods

Several components of behavior were compared between single clutch and mixed broods. The mixed broods were every bit as stable as single clutch broods. Donor goslings obviously came to accept the recipient adults as their parents and responded similarly to the goslings hatched

by the recipient pair. There were no differences in local or daily movements between the two types of broods. Brooding more than eight goslings (even very young ones) is very difficult for a single female. Since goslings likely must be brooded at night and during inclement weather at least during the first week or so, this would limit the northward extension of brood mixing. Even if there was some selective advantage accruing to brood mixing, it could be offset by gosling mortality due to exposure. However, the larger mixed broods were observed forming a brooding mass whereby the female assumed the typical brooding position with a few goslings under the wings and the rest of the goslings crowded in close to her body. Smaller goslings were generally closer to her body or wedged in under or between larger goslings. The relative efficiency of this type of brooding compared to the usual situation is not known, but it is obviously effective at the latitude of Dowling Lake where mortality among goslings in mixed broods was little different from that in single broods. Ganders were never observed brooding.

The exact age at which goslings became aggressive towards siblings and other goslings was not determined but beak to beak fighting was observed in goslings less than a week old. Fighting was much more prevalent in mixed broods than in sibling broods and very often fights were between goslings of different ages indicating non-sibling fights. Fighting generally subsided after a few days when the goslings were about 10 to 14 days old or after the donor goslings had been with the recipient goslings for a few days. Radesater (1973) found agonistic tendencies developing in siblings of Canada geese during the first 2 days after hatching. This agonistic behavior often led to fighting in subsequent days. After about a week the number of fights showed a decrease and by 12 days of age were

almost non-existent. Contrary to other authors he found that a rank order was established among siblings and that this rank order was displayed later in the cackling ceremony. He also said the rank order is only expressed in connection with fights or the cackling ceremony. He did not work with non-sibling geese but they must have been undergoing the same development in mixed broods at Dowling Lake. Although sibling fighting is reduced to an almost non-existent level by age 12 days, there was fighting between siblings and intruders (donor goslings) whenever brood mixing took place. Since the donor goslings were very often smaller than the recipients, it is likely that they attained a lower social rank than that of the recipients. Radesater (1973) also mentioned that this rank is retained into adulthood. The implications of this will be discussed later.

Donor goslings (always less than 5 days old) were accepted into other broods with goslings up to the age of 20 days. The experimentally introduced goslings (up to 15 days old) were accepted into broods similar in age in 1974. Goslings 5 days or older apparently recognize their parents, and thus avoid becoming donors, but have not yet developed aggressive behavior that might prevent brood mixing. As described previously some adults prevented strange goslings from joining their broods when their own goslings were very young, but other adults accepted goslings when their own young were up to 3 weeks old. The greeting ceremony, as described by Balham (1954), appeared in the goslings when they were 3 to 4 weeks old in both sibling and mixed broods. Radesater's (1973) work showed this was a gradually developing process. Fischer (1965:258) demonstrated that the development and repetition of the triumph ceremony

in goslings was of fundamental importance in promoting family unity. It would seem then that once family solidarity is assured and social rank has been established (about 3 to 4 weeks after hatching), the brood, including parents and goslings, rebuffs attempts by younger goslings to join their broods. This was not really tested at Dowling Lake simply because there were very few donors available at the time when most broods were 3 to 4 weeks of age. Transplants in Alberta of goslings 7 to 8 weeks of age showed quite clearly that these goslings were not accepted as part of any of the broods of resident goslings (Surrendi 1970, personal observation). Raveling (1970) found the dominance hierarchy in Canada geese to be ranked: larger family over smaller family over pair over single. This was certainly true at Dowling where large broods won 87 percent (sample size 131) of all interactions with smaller broods. Thus the mixed broods were almost always higher in social rank than single family broods.

Extent of Brood Mixing

Large mixed broods were first observed at Dowling Lake by Ewaschuk (pers. comm.) in 1969. Westworth (pers. comm.) also noticed the occurrence of mixed broods in 1970. Neither had data on the extent of this phenomenon. Table 10 depicts the extent of brood mixing at Dowling Lake during 1971 to 1974. The "mean brood sizes for single broods" were obtained during the first week after hatching whereas the means for "all broods" and "mixed broods" were obtained about 3 weeks after hatching. Thus the mean single brood sizes could be comparatively higher since they eliminate a potential 2 weeks during which mortality could take place.

The mean brood size for single family broods was significantly lower

Table 10. Extent of brood mixing at Dowling Lake in 1971 to 1974.

Year	No. Broods Produced[a]	Donor Broods		Broods Involved in Mixing[b]		Mean Brood Size For Single Broods (Class Ia)	Mean Size For All Broods[c]	Mixed Broods[c]	
		No.	%	No.	%			No.	Mean Size
1971	75	39	52	48	64	4.5 (19)[d]	9.2 (31)[d]	9	21.6
1972	43	11	25	16	37	3.6 (16)	4.4 (23)	5	9.0
1973	82	38	46	51	62	4.5 (17)	7.6 (35)	13	15.1
1974	78	32	41	51	65	4.4 (15)	6.8 (27)	19	10.0
Total	278	120	43	166	53	4.3 (67)	7.2 (116)	46	13.6

a Estimated from hatching success

b Includes both donor and recipient broods

c Calculated from broods about 3 weeks old

d Number of broods used to determine the mean is in parentheses

than the mean size for all broods and the mean size for mixed broods (Table 10). Mixed brood sizes ranged from 8 to 45 in 1971, 5 to 16 in 1972, 5 to 59 in 1973 and 6 to 29 in 1974. The number of broods lost and the number of broods involved in brood mixing were very similar during 1971, 1973 and 1974, but all three years were significantly higher than 1972 (Table 10). The extent of brood mixing, as reflected by the percentage of broods lost and the percentage of broods involved in mixing, appears to be proportional to the numbers of broods produced on the study area. This is logical since fewer broods would have less potential interbrood contact in a given time period; thus the smaller mean mixed brood size. The reason for the similarity in mean mixed brood size between 1972 and 1974 is not known since the incidence of brood mixing was very different.

Brood mixing on the Spondin Lakes, which produced 22 broods in 1972 and 8 in 1973, involved only 4 broods (13 percent) during these years. The two incidents of brood mixing took place on the lake with the smallest brooding area and the greatest number of broods (6 in 1972 and 5 in 1973), further indicating that brood mixing is proportional to the number of broods produced per unit area. The geese on the Spondin Lakes showed much less tolerance toward nearest neighbors during nesting than those on Dowling Lake. This may carry on into the early brooding period, reducing the chances of any aggregation at this time and hence preventing a higher incidence brood mixing. The Spondin broods flocked together when the goslings were older just as the Dowling geese did.

Statements on the occurrence of brood mixing in Canada geese can be found throughout the literature, but none of the authors discuss the quantitative extent and impact of brood mixing. Raveling (1966:54-55)

says:

> "Extensive brood-mixing has occurred in situations where one or a combination of the following relatively 'artificial' or unusual conditions prevailed: geese were introduced, captive, or semi-tame; densities of nesting geese were far higher than those associated with most naturally occurring populations; succeeding generations were nesting in close proximity; much contact occurred just after hatching. Brood-size data are scarce for natural occurring Canada goose populations in the Arctic and Subarctic but no evidence exists to indicate that brood-mixing is a common phenomenon. Mechanisms which prevent brood-mixing of adults with very young goslings probably do not exist in Canada geese because they have never been selected for, as this is basically a species that has evolved under conditions that lead to nesting in low densities. It is concluded that brood-mixing is an aspect of relatively abnormal conditions with respect to the basic nature of the evolution of behavior of Canada geese."

I do not feel that his basic hypothesis holds true for Canada geese nesting in the prairie region of Alberta. My own observations and information collected on the distribution, numbers and productivity of large Canada geese in central and southern Alberta in 1973, 1974 and 1975 by Cole (1973, 1975, 1976) indicate the widespread occurrence of brood mixing in these regions. Quantitative data similar to the Dowling Lake study are not available. The Alberta populations of the Canada geese in question were not introduced, captive or semi-tame although they do nest in dense associations and succeeding generations probably do nest in close proximity leading to much contact between broods after hatching. This, however, is a very natural situation where water bodies are scarce and secure nesting sites are limited to island situations and thus one would expect dense nesting associations. There is no reason to believe that these geese have not been nesting here for centuries, but the recent proliferation of Ducks Unlimited (Canada) and irrigation district water impoundments has undoubtedly provided numerous new nesting opportunities. The possible

implications of brood mixing will be elaborated in the concluding discussion of this paper.

Brood Production and Survival

Tables 2 and 3 outline the success of nesting at Dowling Lake. They show that the average success over an 8-year period was about 63 percent, with variations between years the result of such factors as predation. Thus almost 40 percent of the production was lost before any goslings left the nest. If the years of heavy coyote predation, 1968 and 1972, are eliminated, then the average hatching success was about 75 percent or 25 percent of the potential production was lost before hatching. Table 11 summarizes what happened to the goslings from successful nests. Data were complete only during 1971, 1972 and 1973. The percentage of eggs not hatching in successful nests was not significantly different between years except in 1972 which was higher than all other years. The poor hatching success in 1972 is attributed to the use of embryo dyes. Estimated mean brood sizes, based on the number of eggs hatched per nest, were always higher than the means for single broods observed within the first week after hatching except in 1970 when there was no apparent difference. This represented an immediate annual post hatch loss of 2.2 to 12.3 percent of the goslings. Further losses occurred when entire broods were not accounted for in 1971 and 1973. It is not known whether this loss is real or the broods were just not observed on the study area. The combined losses attributed to unsuccessful nests, unhatched eggs in successful nests and early gosling mortality averaged 49 percent of the potential production over the years for which the data is available. During 1971, 1972 and 1973 about 41, 76 and 39 percent

Table 11. Production and survival of goslings of Canada geese at Dowling Lake in 1967 to 1974.

Year	Mean Clutch Size	% Eggs Not Hatching	Mean Brood Size			Number of Broods			Number of Goslings		
			Est'd[e]	% Goslings Lost	Obsv'd[f]	Est'd[e]	% Broods Not Accounted For	Obsv'd[f]	Est'd[e]	% Prod Lost	Obsv'd[f]
1967[a]	4.4(96)[d]	-	-	-	-	58	-	-	-	-	-
1968[b]	5.4(94)	-	-	-	-	34	-	-	-	-	-
1969[a]	5.2(53)	-	-	-	-	79	-	-	-	-	-
1970[c]	5.3(38)	6.5	5.0(17)	0	5.0(31)	83	-	-	415	-	-
1971	5.6(70)	10.7	5.0(51)	10.0	4.5(19)	78	3.8	75	390	13.3	338
1972	5.2(45)	21.1	4.1(26)	12.3	3.6(16)	42	0	42	172	12.1	151
1973	4.9(83)	6.1	4.6(73)	2.2	4.5(17)	87	5.7	82	400	7.8	369
1974	4.8(67)	4.2	4.6(64)	4.3	4.4(15)	81	-	-	373	-	-
Means	5.0(493)	8.2	4.7(231)	4.8	4.5(98)	68	4.8	66	350	10.9	286

a Data from Ewaschuk (pers. comm.)
b Data from Vermeer (1970)
c Data from Westworth (1970)
d The number of samples used to derive the mean is in parentheses
e Estimates are based on hatching success
f All broods and goslings were Class Ia when observed

respectively of the eggs laid failed to produce goslings about 5 days old. Gosling mortality from age 5 days to 5 weeks was only studied during 1972 and 1973.

Gosling mortality was calculated using known single family broods or mixed broods whose makeup was known. Mortality of single family broods and mixed broods was compared to see if selection might be favoring one group over the other. Mortality was 4.9 percent in 1972 and 23.8 percent in 1973 if single and mixed broods are lumped together. In 1972 single brood gosling mortality was negligible compared to 9.3 percent for mixed broods, but the impact on the population (about five goslings less) was small since production was poor that year and brood mixing was not as prevalent (Table 10). Mortality within single family broods (25.4 percent) and mixed broods (21.2 percent) was very similar in 1973. The two years, 1972 and 1973, were very different so it is not known which, if either, represented an average year, but there is no strong indication that survival favors either single family or mixed broods. Mortality from age 6 weeks to flight at 9-10 weeks was not monitored closely, but goslings 6-8 weeks old, marked during banding, had less than a 1 percent mortality rate. This means in an average year, when about 100 pairs nest, the production at Dowling Lake is about 250 flying juveniles. Total production on the Spondin Lakes was highly variable (Table 4) but gosling survival, about 95 percent, was high in both years. Clutch and brood sizes for single families were consistently higher than at Dowling Lake. The significance of this is not known.

F. Behavior of Subadult Geese

Subadults were those geese that did not establish a nesting territory that led to subsequent production of eggs. It was assumed these birds had not bred previously, but the status of many of them was not known. The subadult group of geese at Dowling Lake included known 1-, 2- and 3-year-olds.

Homing of transplanted juvenile Canada geese was studied by Surrendi (1970) in 1968 and 1969 about 40 kilometers east of Dowling Lake. He found that 25 percent of the yearling females homed to the area around their release sites, while a significantly smaller proportion, 17 percent, of the males did so. During the 4 years of this study 21 percent (38 of 175) of the yearling females homed to Dowling Lake, while a significantly lower proportion, 9 percent (18 of 189), of the males did so. Assuming the juvenile mortality was similar to that found by Surrendi (1970), about 50 percent after the breeding season, then 19 percent of the yearling males and 43 percent of the yearling females had returned to Dowling Lake the following spring. The fate of the other yearlings that were still alive is not known. Some of these birds were undoubtedly on the study area and just not observed. A small number were accounted for when they returned to Dowling as 2-year-olds the following year. Homing in 2-year-old females was higher at Dowling Lake, 16 percent (18 of 116), than that reported by Surrendi (1970), 7 percent (5 of 68). Surrendi (1970) had no 2-year-old males home whereas 4 percent homed to Dowling. However, 2-year-olds have been through two seasons of hunting mortality. If this mortality is assumed to be constant at 50 percent per year, then the actual homing of 2-year-old females has increased from 43 percent as yearlings to 62 percent (18 of 29)

as 2-year-olds. This would be 17 percent (5 of 29) for 2-year-old males compared to 19 percent for yearling males. Sample sizes are too small to analyze the data for 3-year-olds. The percentage of marked geese that lost collars was ignored because it was not known. It seems then that females show significantly greater homing tendencies than males to the area where they were hatched. Surrendi's (1970) data showed that they homed to the area where they fledged even if they had not been hatched there, so it is likely that the familiarity with the area, gained during the period immediately after beginning to fly, is important.

No yearlings of either sex were known to nest during this study. About 33 percent of the returning 2-year-old females nested; the rest remained as non-breeding subadults. No 2-year-old-males held a nesting territory. All known 3-year-old females nested while only one 3-year-old male did, but sample sizes were very small. Wood (1965), studying the development of the reproductive organs in Canada geese, said that both sexes were immature in their first year, and that in their second year most males were physically mature while females were not. All 3-year-olds were physically mature, but when placed under crowded conditions, did not nest even though the gonads matured normally (Wood 1964). Balham (1954) and Collias and Jahn (1959) found a very small percentage of 2-year-olds nesting, but Brakhage (1965) and Sherwood (1967) indicated that 33 percent and 80 percent respectively of the 2-year-olds they studied had nested. It appeared that 2- and 3-year-old females were physically mature at Dowling but 2-year-old females, potentially capable of breeding, were suppressed from doing so under crowded conditions. The fact that only 33 percent of the 2-year-old females nested is one indication that conditions were relatively crowded at Dowling Lake and that pairs were not nesting because

they were unable to obtain a nesting territory with a suitable nest site. One example of this occurred when an adult female, that had nested successfully in 1972, paired with a 2-year-old male in 1973. They tried repeatedly to secure a territory near her previous year's nest site but were unable to do so; the female did not nest that season.

Pairing tendencies of Canada geese have been discussed by many authors (Martin 1964, Brakhage 1965, Raveling 1967, Sherwood 1967, Raveling 1969b and others). Martin (1964) and Sherwood (1967) both suggested that yearling pairs represented only short-term associations that were terminated with the onset of the molt. Brakhage (1965:756, Table 3) said that 42 percent of the males and 14 percent of the females paired as yearlings. Brakhage (pers. comm., Raveling 1969b) also said that marked yearlings, paired in summer, did not associate the following winter, but the same two geese often paired in a lasting association in late winter-early spring at the onset of their 2-year-old season. Raveling (1967, 1969b) concludes that the majority of yearlings (1+ years) were singles in winter and began the spring migration as such.

Pairing of yearling Canada geese in Alberta was discussed by Ewaschuk (1970) and Surrendi (1970). Ewaschuk (1970:40) observed short term associations between yearlings, or between older geese and yearlings similar to that found by Balham (1954). Surrendi (1970:728, 730) found that 80 percent of the yearling females and 68 percent of the yearling males formed observable pair bonds during 1968 and 1969. He also said that much of the pairing appeared to take place on the breeding ground, but later-arriving yearlings were more often paired than earlier arriving birds. Instability of yearling pair bonds was also apparent during his study.

Ninety-three percent (31 of 32 females; 10 of 12 males) of the year-

lings observed at Dowling Lake in 1972 and 1973 appeared to be paired. Only 3 of the 44 marked yearlings had marked mates. One of these pair bonds remained intact throughout the observation period, that is, until the molt migration, while the other two bonds appeared to dissolve earlier. The three unpaired yearlings usually associated with other pairs when they were tolerated, or remained off by themselves. All the yearlings flocked together in late May-early June with the other molt migrants in preparation to leave the study area. Pair bonds were not obvious at this time but still may have been in existence.

Of 13 known 2-year-olds, six appeared paired on arrival and the rest paired very quickly after arrival. All known pair bonds involving 2-year-olds remained stable throughout the observation period. Brakhage (1965) and Surrendi (1970) also found a high incidence of stable pair bonds in 2-year-olds. It would seem that some pairing must take place during the spring migration to account for the gene mixing that occurs when males from one area mate with and return to the natal areas of the females they pair with. The evidence at Dowling suggests that very few males hatched there actually breed there but sample sizes were too small for the evidence to be conclusive.

I found, similar to Ewaschuk (1970), that paired subadults carried out most of the activities of breeding geese but were less vigorous and spent less time at them. Subadult ganders often defended the area around the pair wherever they happened to be, but this could easily be followed by two pairs loafing together less than 2 meters apart. Two copulations between subadults were observed. They often tested established territory holders but rarely won these encounters. Subadult females regularly made nest scrapes and one yearling female made 23 different scrapes during a 3-day period. On three occasions in 1972 and 1973 nesting adult females

were left unattended by their ganders and non-breeding subadults drove the resident female off. The subadult female incubated the unattended eggs in all three cases; one for only 3 minutes, one for 13 minutes and one for 87 minutes. The first two females appeared to tire very quickly and the pair left on their own before the residents returned, but the third female remained on the eggs for 87 minutes until the resident gander and female returned to drive the pair off. Subadults were not tolerated within the nesting territories of resident geese regardless of their age, sex or paired status. This was contrary to the observations of Brakhage (1965) and Surrendi (1970) who found that non-breeding females were tolerated near the nest, but similar to observations by Ewaschuk (1970) in 1969 at Dowling Lake. However, this intolerance of subadults broke down after hatching when most pairs allowed subadults to approach within 3-5 meters of their brood. Experience gained by "practising" the behavioral patterns associated with breeding may provide valuable conditioning for future nesting in a dense nesting association such as Dowling Lake. Breeding behavior and aggressive tendencies subside quickly as the subadults flock together for the assumed molt migration. About 10 subadults remained on the study area to molt each year.

G. Population Dynamics During the Non-Breeding Season

The study at Dowling Lake showed that on the average 100 pairs of geese nest annually and produce 250 goslings to flight. The primary cause for mortality after this time is harvest by hunters. Table 12 shows the composite dynamic mortality rate estimates from shot recoveries of Canada geese banded and released as locals on Dowling Lake during 1969-1973. The mortality rate for juveniles (immatures), 52.2 percent, is similar to that found in many other studies of Canada geese (Chapman et al. 1969:34), but the mortality rate for adults, 51.9 percent, is much higher than expected. Several authors (Hickey 1952, Haldane 1955, Geis 1959 and others) have suggested that small sample sizes with incomplete data, such as that in Table 12, result in inflated mortality rates. Table 13 indicates the number of collared adults sighted at Dowling Lake one year after they were marked. Using these data the maximum annual mortality rate possible for this adult cohort was 51.3 percent, and this makes no allowance for collar loss and returning collared adults that were never sighted. The direct recovery rate for juveniles, 0.1417, was slightly higher than that for adults, 0.1379, also indicating that the mortality rates in Table 12 may be incorrect. Because the calculated mortality rate seemed too high, several theoretical population models were constructed assuming the population was stable.

The only known information used was that 100 pairs produced 250 goslings to flight. Maximum allowable mortality rates under different assumptions appear in the models to follow. Age classes will be designated as follows: A - adult, J - juvenile or immature, Y - yearling and 2Y - 2-year-old. All birds 3 years or older were classed as adults.

Table 12. Composite dynamic mortality rate estimates from shot recoveries of Canada geese banded and released as locals on Dowling Lake during 1969-1973.

Banding Year	Number Banded	Number of Recoveries Per Recovery Year						First Hunting Season Recovery Rate
		1	2	3	4	5	6	
1969	89	20	12	5	3	1	2	0.2247
1970	165	25	15	6	3	3	0	0.1515
1971	129	23	5	3	0	0		0.1783
1972	20	4	2	2	1			0.2000
1973	146	15	9	1				0.1027
Totals	549	87	43	17	7	4	2	0.1585
Banded Birds Available		549	549	549	403	383	254	
Recoveries Per 1000 Banded		158.5	78.3	31.0	17.4	10.4	7.9	
No./1000 Alive Going Into Period		303.5	145.0	66.7	35.7	18.3	7.9	

Juvenile (imm.) mortality rate $= \frac{158.5}{303.5} = 0.5222$

Yearling mortality rate $= \frac{78.3}{145.0} = 0.5400$

Adult mortality rate $= \frac{66.7}{128.6} = 0.5187$

Average annual mortality rate $= \frac{303.5}{577.1} = 0.5259$

Table 13. Number of collared adults sighted at Dowling Lake one year after they were marked.

Year	Number of Adults Collared	Number of Collared Adults Sighted One Year Later	Percent Adults Returning
1969	7	4	57.1
1971	28	13	46.4
1972	14	6	42.9
1973	27	14	51.9
Total	76	37	48.7

Population Model A

This population is based on the following assumptions:

1. Mortality is constant for all age cohorts.
2. No breeding takes place until 3 years of age.
3. All birds 3 years and older breed.
4. The population size remains constant.
5. Two hundred adults produce 250 juveniles annually.

Therefore, the maximum allowable mortality rate is 34.7 percent. This population would appear as follows:

	A	J	Y	2Y
Number Alive After Breeding Season	200	250	163	107
Number Alive After Annual Mortality	130	163	107	70
Number Alive After Next Breeding Season	200	250	163	107

This population model is based on the results from Table 12 where mortality rates for all cohorts were almost constant around 50 percent. This theoretical population shows that the population would very quickly become extinct at a constant mortality rate of 50 percent because 34.7 percent is the maximum allowable loss. In order to maintain a stable population at a 50 percent loss rate, the 100 pairs of adults would have to fledge about 600 juveniles annually; this is greater than the number of eggs laid. Since the population was not declining, either Table 12 is incorrect or there was large scale immigration. Few geese banded at other locations were retrapped at Dowling Lake indicating that immigration was probably not significant. Population model B is slightly more complex.

Population Model B

This population is based on the following assumptions:

1. The mortality rate is 50 percent for juveniles and constant for all other age cohorts.

2-5. Same as population A.

Therefore, the maximum allowable mortality rate for all age cohorts other than juveniles is 30.3 percent. This population would appear as follows:

	A	J	Y	2Y
Number Alive After Breeding Season	200	250	125	87.1
Number Alive After Annual Mortality	139.4	125	87.1	60.6
Number Alive After Next Breeding Season	200	250	125	87.1

The mortality rate for juveniles is close to that in Table 12 and close to that possible for a population of this type, but for the other age cohorts it is well below that suggested in Table 12. This is still a rather simple model and led to construction of population model C, a more complex model.

Population Model C

This population is based on the following assumptions:

1. The mortality rate is 50 percent for juveniles, 40 percent for yearlings and constant for all other age cohorts.
2. Yearlings do not breed but 33 percent of the 2-year-olds do.

3-5. Same as population A.

Therefore, the maximum allowable mortality rate for all other age cohorts is 30 percent. This population appears as follows:

	A	J	Y	2Y
Number Alive After Breeding Season	200	250	125	50
Number Alive After Annual Mortality	140	125	25+50=75	35
Number Alive After Next Breeding Season	200	250	125	50

This model is very likely getting close to the actual situation at Dowling Lake. The annual production and the percent 2-year-olds breeding are both known. All indications were that, if anything, this population had a breeding surplus, because only 33 percent of 2-year-old females breed. Therefore, the model seems more representative of this population of geese than the band return data.

The percentage of bands turned in for the 1969-1972 banding cohorts, assuming all bands from these cohorts are now turned in, was 39.3 percent. The other 60.7 percent of the bands were lost due to crippling losses, natural mortality and failure of hunters to report bands. Using the data as is, with no adjustment for crippling loss or natural mortality, and the data from Table 12, the mortality rates would be 36.1 percent ($\frac{100}{39.3}$ x 14.2) for juveniles and 35.1 percent ($\frac{100}{39.3}$ x 13.8) for adults. Natural mortality is unknown. Crippling losses for the Dowling Lake goose population are not known but Hopper et al. (1975) calculated an average loss of 22% for mallards (Anas platyrhynchos) in Colorado. If this is applied to geese, the number of bands then accounted for is (39.3 plus $\frac{22}{100}$ x 39.3) 47.9 percent. The adjusted mortality rates would then be 29.6 percent ($\frac{100}{47.9}$ x 14.2) for juveniles and 28.8 percent ($\frac{100}{47.9}$ x 13.8) for adults. The preceding calculated mortality rates seem more realistic than Table 12 and certainly come close to or less than the allowable loss rates for a stable population as outlined in the three models. It is possible that the long term average production was higher than 250 juveniles annually as was the case during the 3 years of this study. This would mean that allowable mortality rates could be somewhat higher than those predicted in the population models.

Ewaschuk and Neave (1970:24) indicated an average annual mortality of 46 percent (50.7 for juveniles and 42 percent for adults) for Canada geese breeding in the Eastern Irrigation District of Alberta from 1955 to 1962. This population would require a production of about 350 juveniles per 100 breeding pairs annually to sustain itself with the same assumptions as numbers 2-5 in theoretical population C. This would mean, however, that nesting success and gosling survival could not go much below 65 percent which seems possible in that area. Thus the banding data for central Alberta and Dowling Lake gives an indication of hunting mortality rates but they are most likely too high since the population appears to be stable in some localities and on the increase in others, whereas the banding data suggests it should be decreasing.

There was no difference in direct recovery rates between single family goslings, 0.1374 (18 of 131), and mixed brood goslings, 0.1149 (10 of 87), but the sample sizes are quite small. However, this does indicate that there is probably no differential hunting mortality between large mixed broods and single family broods.

Band recoveries also provide information on the distribution of the harvest, the timing and location of the fall migration and the location of the wintering areas. The magnitude of the recoveries from any one area is a function of not only how many birds are there but also how much hunting pressure there is. Thus the data must be interpreted carefully. Recoveries outside the hunting seasons were negligible. There were a few collar sightings and retraps but they did not change the picture so they are not included in this discussion.

Table 14 gives a summary of Dowling Lake Canada goose band recoveries by date and locality. It is apparent that most of the Dowling Lake flock

Table 14. Band recoveries of Canada geese banded at Dowling Lake in July of 1969-1975.

Location	Number of Band Recoveries for Each Time Period											Total Number of Band Recoveries	Percent of Total Recoveries
	September 1-15	September 16-30	October 1-15	October 16-31	November 1-15	November 16-30	December 1-15	December 16-31	January 1-15	January 16-31	Feb. 1-15		
Pacific Flyway													
Idaho	0	0	0	0	0	3	4	1	1	0	1	10	4.3
Oregon	0	0	1	0	1	0	0	0	0	0	0	2	0.9
Utah	0	0	0	0	0	1	1	0	0	0	0	2	0.9
Nevada	0	0	0	0	0	0	0	1	0	0	0	1	0.4
California	0	0	0	0	0	1	0	3	2	1	0	7	3.0
Subtotal	0	0	1	0	1	5	5	5	3	1	1	22	9.5
Central Flyway													
Alberta	9	14	27	10	5	1	0	0	0	0	0	66	28.4
Sask.	0	2	3	4	1	0	0	0	0	0	0	10	4.3
Montana	0	0	1	2	5	3	0	1	0	0	0	12	5.2
S. Dakota	0	0	0	1	0	0	1	0	0	0	0	2	0.9
Wyoming	0	0	0	0	0	0	1	1	0	0	0	2	0.9
Nebraska	0	0	0	0	0	0	2	0	0	0	0	2	0.9
Colorado	0	0	0	0	10	12	26	41	13	8	0	110	47.4
Kansas	0	0	0	3	0	0	0	1	0	0	0	4	1.7
N. Mexico	0	0	0	0	0	0	0	0	0	1	0	1	0.4
Texas	0	0	0	0	0	0	0	1	0	0	0	1	0.4
Subtotal	9	16	31	20	21	16	30	45	13	9	0	210	90.5
Total	9	16	32	20	22	21	35	50	16	10	1	232	100.0

is present in Alberta during September and October leaving the province during late October-early November. There are very few band returns between central Alberta and the two wintering areas, Colorado and Idaho-California, probably reflecting lower hunting pressure and relatively quick passage through the areas between. Figure 15 shows the distribution of the band recoveries in Canada and the United States. There were almost seven times as many returns from the central flyway as the Pacific flyway (Alberta returns were excluded), but this may be misleading since the hunting pressure around the Denver-Fort Collins, Colorado wintering areas is probably much higher than that in the Pacific wintering areas. About 33 percent of the harvest is in Canada while 67 percent is in the United States; Alberta and Colorado accounting for about 76 percent of the total kill. The recoveries were divided into different age cohorts (Table 15) to see if they were migrating at different times. It is obvious both from Table 15 and Figure 15 that the molt migrants move along the same routes and at the same time as the rest of the Dowling Lake flock. Whether they move with each other is not known but it seems likely. There were no band returns to confirm the molt migration. It appeared the molt migrants were already back to the study area before the hunting season opened. It is also evident that the Dowling Lake population migrates in smaller sub-flocks as returns from the same age cohorts were occurring simultaneously in widely separated localities (e.g. Alberta and Colorado). When the Dowling Lake geese leave the wintering grounds and what routes they follow during the spring migration are not known, but they arrive back on the breeding islands in March and April.

Figure 15. Locations of band recoveries of Canada geese banded at Dowling Lake in July of 1969-1975.

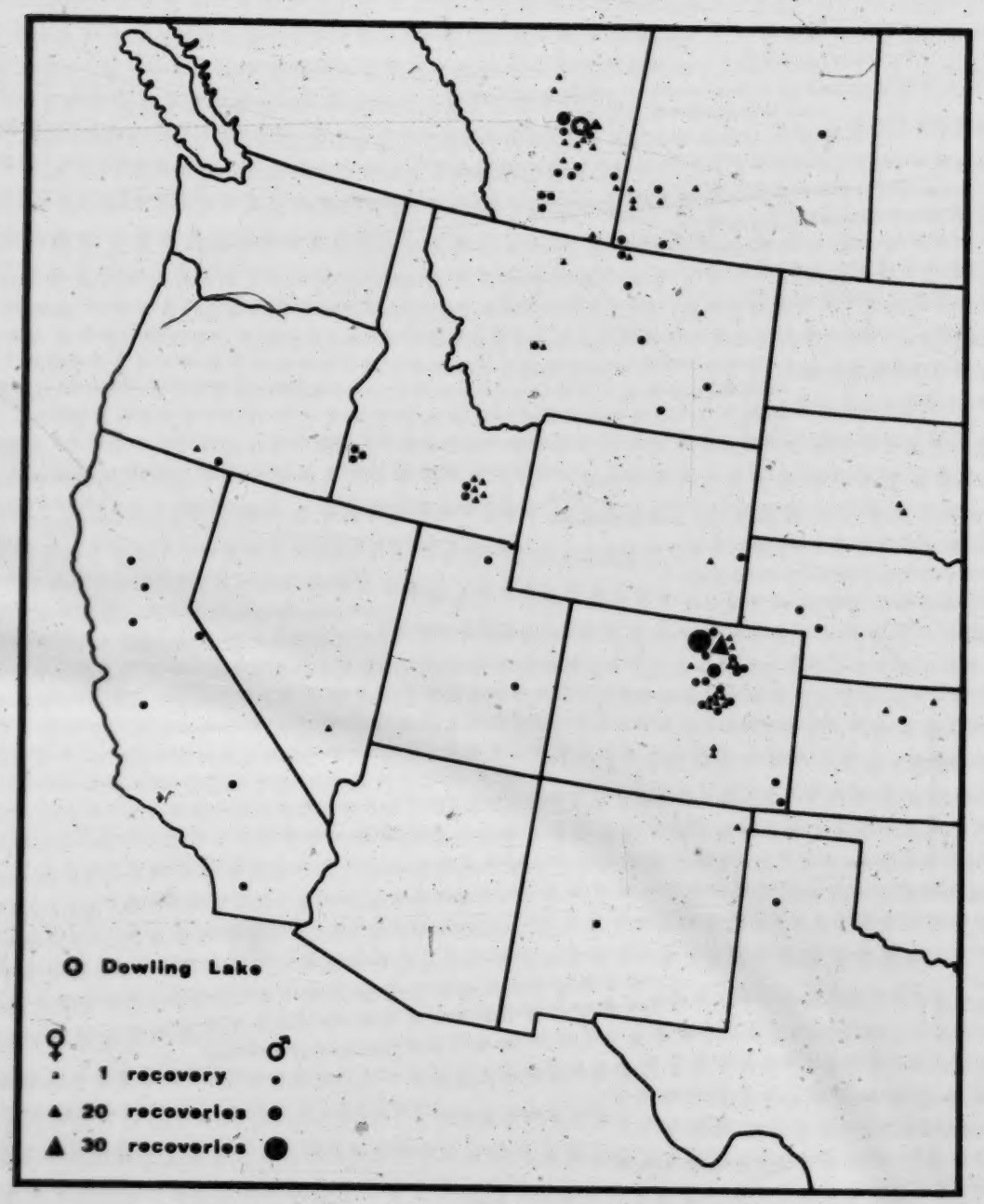
Dowling Lake
♀
♂
1 recovery
20 recoveries
30 recoveries

Table 15. Band recoveries by age, date and location for Canada geese banded at Dowling Lake in July of 1969-1975. Only those states and provinces with 5 recoveries or more are shown.

Location	Age	Number of Band Recoveries for Each Time Period											
		September		October		November		December		January		Feb.	
		1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	Total
Alberta	J	4	10	13	2	4	0	0	0	0	0	0	33
	A	4	0	7	4	0	0	0	0	0	0	0	15
	Y	0	4	6	4	1	1	0	0	0	0	0	16
	2Y	1	0	1	0	0	0	0	0	0	0	0	2
Sask.	J	0	0	0	1	0	0	0	0	0	0	0	1
	A	0	0	1	1	0	0	0	0	0	0	0	2
	Y	0	1	2	2	1	0	0	0	0	0	0	6
	2Y	0	1	0	0	0	0	0	0	0	0	0	1
Montana	J	0	0	0	1	3	1	0	0	0	0	0	5
	A	0	0	0	0	2	2	0	0	0	0	0	4
	Y	0	0	0	1	0	0	0	1	0	0	0	2
	2Y	0	0	1	0	0	0	0	0	0	0	0	1
Colorado	J	0	0	0	0	7	6	17	29	10	4	0	73
	A	0	0	0	0	2	2	3	6	1	0	0	14
	Y	0	0	0	0	0	3	5	4	1	4	0	17
	2Y	0	0	0	0	1	1	1	2	1	0	0	6
Idaho	J	0	0	0	0	0	0	0	1	0	0	0	1
	A	0	0	0	0	0	1	2	0	1	0	1	5
	Y	0	0	0	0	0	0	1	0	0	0	0	1
	2Y	0	0	0	0	0	2	1	0	0	0	0	3

continued . . .

Table 15 Continued.

Location	Age	Number of Band Recoveries for Each Time Period											
		September		October		November		December		January		Feb.	Total
		1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	
California	J	0	0	0	0	0	0	0	2	0	1	0	3
	A	0	0	0	0	0	1	0	0	2	0	0	3
	Y	0	0	0	0	0	0	0	1	0	0	0	1
	2Y	0	0	0	0	0	0	0	0	0	0	0	0
Totals	J	4	10	13	4	14	7	17	32	10	5	0	116
	A	4	0	8	5	4	6	5	6	4	0	1	43
	Y	0	5	8	7	2	4	6	6	1	4	0	43
	2Y	1	1	2	0	1	3	2	2	1	0	0	13

CONCLUDING DISCUSSION

The purpose of this study was to examine the factors affecting survival in this population of Canada geese, especially during the brood rearing period. The chronology of events during the breeding season at Dowling Lake was discussed. Timing of events was linked to early spring weather, but weather itself did not directly affect production. However, by lowering water levels in 1968 and delaying the melting of the ice in 1972, weather indirectly affected production by allowing coyotes access to the normally secure large nesting island. Predation was insignificant in other years of the study but 50 and 46 percent of the potential production was destroyed by coyotes in 1968 and 1972, respectively, through destruction of the nests. Early spring spacing behavior was studied in 1971 to see if and how this might affect the final spatial distribution of nesting territories on the large island. The conclusion was that it had little impact. Pairs did not appear to seek out and compete for early snow-free locations. Early established territories were larger but decreased in size with the encroachment of later nesting breeding pairs.

Some of the behavioral studies done by Ewaschuk (1970) were repeated in 1971. Results were very similar. Pairs that deserted their nests usually lost more interactions than they won and had smaller territories. Unsuccessful pairs had significantly lower nearest nest distances indicating that these geese may have been of lower dominance status with smaller territories. The presence of the gander on the territory was the most important factor in maintaining the territory and thus the nest site. Ganders often left the territory for no apparent reason and did not return. It seems possible that because they had smaller territories

(that is, lower dominance), they may have become so run down during the early incubation period that they had to leave in order to survive, or they may have been inexperienced and just lost interest. This aspect requires further study. During the years that data was available, 1967-1974, desertion accounted for losses of 3 to 27 (mean of 14) percent of the nests.

The original reason for constructing wooden platforms on the large island in Dowling Lake was to vertically stratify nesting territories (that is, ground nesters and platform nesters) thereby decreasing territory size and increasing nesting densities. This did not work and platform nesting had no significant impact on production in this population. Early indications were that the nesting population could be increased if the platforms were placed over water, but a durable platform that could resist changing water levels and ice damage was not found and the experiment was discontinued.

The study of brood behavior was the major thrust of the work on Canada geese at Dowling Lake during 1971-1974. Brood mixing, where the goslings hatched by one pair join the brood accompanying another pair, was very common and was examined closely to see how it occurred and what effect this had on the population. Because the broods tended to aggregate and utilized very restricted brood rearing areas, the number of interbrood contacts was very high and hence the high incidence of brood mixing. The extent of mixing was proportional to the number of broods on the brood-rearing areas. Thus brood mixing was probably a phenomenon resulting from chance encounters between broods aggregating on the same area, and not a result of dominant geese seeking out and "stealing" goslings from less dominant pairs. During six of the seven

brood takeovers observed, there was no obvious dominance by the recipient pair. In one case the recipient gander actually chased the donor pair away from their goslings and the donor goslings then joined his brood, but in the other six cases it was the goslings that moved away from their own parents to join the recipient brood with the donor parents not being dominated in any observable way. Donor goslings were always less than about 5 days old but recipient goslings ranged in age from 3 to 20 days. Radesater (1973) said that fighting between siblings of Canada geese was very common at an early age and quickly led to a dominance hierarchy within the brood that was later evident in the cackling ceremony. Fighting was significantly higher in mixed broods between donor and recipient goslings than between siblings. This likely established the position of the donor goslings within the dominance hierarchy as little fighting was observed in older mixed broods. Whether donor goslings enjoyed a lower or higher dominance status in the mixed broods was not determined. Although mortality during the brood-rearing period was slightly higher for mixed than sibling broods in 1972, there was no difference in 1973 and no difference when the two sample years were lumped. There is considerable room for speculation because the impact of brood mixing on the Dowling Lake Canada goose population is unclear.

There are three possible explanations for brood mixing as follows:

1. It is a phenomenon of sufficiently recent occurrence to preclude any manifestations of selection.
2. It is a phenomenon that has occurred for a long period of time and has been selected for in some populations of Canada geese because of the positive benefits accruing

to it and selected against in other populations because of the negative attributes.

3. It is a phenomenon that occurs but has no significance.

Raveling (1966, 1967) accepts that brood mixing is a common occurrence in some populations of B. c. maxima and B. c. moffitti but suggests that it occurs only in unusual or artificial situations. He suggests that the geese were introduced, captive or semi-tame, the nesting densities were higher than naturally occurring populations and that much contact between families occurred just after hatching. Alberta Canada geese do nest in high densities and much contact between families occurs just after hatching, but I cannot see why this is unusual or artificial, and it would be very difficult to determine what nesting density is natural and what is artificial or unnatural. Raveling also pointed out that some studies of B. c. maxima and B. c. moffitti have not revealed brood mixing (Craighead and Craighead 1949, Balham 1954, Kebbe 1955, Klopman 1958). He suggested that the reason for lack of brood mixing in these populations was that the geese were more dispersed during nesting and firm family bonds develop before extensive contact with other families, and that flock formation occurs when the goslings are 2-3 weeks of age or more. His argument is logical but does not discount the fact that brood mixing may be of some benefit to some populations of Canada geese which are not dispersed during nesting.

Brood mixing may increase survival in both adults and young by leaving more competent pairs in charge of the young; by freeing more adults to participate in the molt migration; by increasing survival of young into adulthood due to better position in the dominance hierarchy; by more effective use of restricted brooding areas and by more effective

predator evasion. Negative aspects that should be discussed in this context are limitations to brooding by the female, greater vulnerability to predators (especially coyotes) due to large size and visibility of mixed broods and the greater possibility of brood disruption with the death of the parents.

There was no clear cut indication that certain pairs were more involved as recipients in brood mixing, but the percentage of adults marked at any one time was small and made it difficult to determine. Collias and Jahn (1959) and Sherwood (1967) indicated older, more dominant pairs were the recipients. This is beneficial to the young because the older, more competent pairs may look after the goslings better and increase their survival. Collias and Jahn (1959) also said that there were habitual losers or donors who continually lost their broods. It is quite possible that these pairs would make poor parents also, but if they can still contribute to production by nesting and hatching young, they are making a useful contribution to the population.

Brood mixing may also free pairs, that are run down physically from defending a territory and incubating eggs, to recuperate quickly and thus increase their own survival. I have no evidence that this is so, but it seems logical that there would be less stress on broodless adults and hence a more rapid physical recovery. Many of the pairs, unsuccessful nesters and those having lost broods, join the assumed subadult molt migration. Sterling and Dzubin (1967) speculated on the survival advantages of molt migrations in Canada geese. They suggested that even with relatively long flights to areas where predator populations are low, visibility is unlimited, grazing foods are common and suitable wetlands for escape are available, survival would be higher than if they had

stayed on the breeding grounds. Perhaps shorter days, competition for food resources and less escape cover make the breeding ground less desirable. Having adults participate in the molt migration may increase survival of the population as a whole. They will know the molt migration route and molting areas better, having participated in previous years, and could lead the younger, inexperienced subadults. The molting group provides the nucleus to restock a breeding area should a short term disaster (for example, dried-up water bodies would make molting adults with broods vulnerable to coyote predation) eliminate most of the successful nesters in any one year.

The large broods may condition the young to tolerate larger, more dense aggregations of geese which would lead to greater tolerance during nesting; that is, smaller territories and fewer serious fights. It has been well established that larger broods have a higher position in the dominance hierarchy than smaller broods (Hanson 1953, Raveling 1970), and that dominance established at a very young age often carries on into adulthood (Radesater 1973). This means that young from mixed broods, especially larger ones, would be more successful due to a higher dominance position in the flock. Raveling (1967, 1969b) said that families of Canada geese remained intact all winter and that larger families were the most dominant. Higher dominance also increases survival if there is any competition for food resources or roosting sites on the wintering grounds. The same may be true on the breeding ground, especially where competition for nesting sites is intense as at Dowling Lake. The continued existence of single brood pairs could probably be attributed to birds immigrating into the Dowling flock from dispersed nesting populations in the surrounding areas. If these pairs remain secretive and avoid other broods during the first

week after hatching, they avoid brood mixing, but their goslings may have a lower dominance rank than those in mixed broods, and ultimately they will be less successful.

Although there was no evidence of food shortage or a shortage of brooding areas at Dowling Lake, it is possible that it occurs in some situations. Having adults and non-breeders leave the area increases the survival of both groups by decreasing the competition for food and space and by decreasing the vulnerability to terrestrial predators such as coyotes. There are two strategies to avoid predation. The first is to stay in small groups that are well dispersed, secretive and hidden in the cover, thereby attracting little attention and avoiding random predator contacts. The second strategy is to join forces and move about in large, obvious groups that are not well hidden but more readily detect any predator approaches and escape easily. Larger broods would thus be more effective in predator evasion, but they can be disadvantageous. A coyote intercepted a large brood of 16 moving between Dowling Lake and lake H (Fig. 13) and caused heavy losses. This type of behavior does not favor the existence of large, visible groups.

Evidence from a study of transplanted Canada geese at Oliver Lake, Alberta suggests that without parental guidance, juveniles suffer much higher hunting mortality than those with parental guidance (Wishart, pers. comm.). Thus it is possible that larger broods could more easily become fragmented with the loss of their parents and suffer high mortality without parental guidance. However, there is some evidence from banding records that the geese from the same breeding population migrate in sub-flocks together, and thus surviving adults other than their parents could provide the necessary guidance. The initial indication at Dowling Lake

was that no difference existed in hunting losses between single family and mixed broods.

The ultimate limitation to brood mixing in many populations would be the limited capability of the female to brood large numbers of goslings. Brooding at night and during inclement weather is likely essential for survival during the first few days of a gosling's life in most northern areas of North America. Thus the limiting factor for the northward or altitudinal extension of brood mixing would be the night temperatures during peak hatching and the week following. All of the preceeding hypotheses on advantages and disadvantages of brood mixing are largely speculative and require testing to determine the cause and effect relationships. However, its widespread occurrence suggests to me that there must be some selective advantages to brood mixing.

Brood mixing or creching has been described in several duck species, including the shelduck Tadorna tadorna (Hori 1964, Williams 1974), the velvet scoter Melanitta fusca (Koskimies 1955), the common eider Somateria mollissima (Gorman and Milne 1972) and others. Hori (1964) suggested that creching allows the parents to leave earlier on their molt migration and increase their chances for survival. Gorman and Milne (1972) argued, "that creching has evolved in eiders where the parent females have to leave their young in order to feed and recover body weight lost during incubation. The role of the 'guard-females' in this situation appears mainly to be that of detecting aerial predators such as gulls or crows." Williams (1974) found that females attending broods survived just as well as those losing broods, duckling mortality was significantly higher in creches than family broods but growth of ducklings was faster in larger creches than in family broods. He felt higher survival of creche

ducklings after fledging, because they were in better condition, might offset the losses attributed to creching. The common theme emerging here is that creching is or may be important to the survival of adults and/or young in some populations of these duck species. Since most duck species do not form close family ties, it is difficult to compare the social implications with those of Canada geese. Brood mixing has not been recorded in other species of North American geese, probably because they are all Arctic nesters and brooding and family integrity are essential for survival.

The study at Dowling Lake revealed that an average of 100 pairs nested annually and laid about 500 eggs. About 50 percent of these eggs resulted in flying juvenile geese. Loss of production up to fledging has been discussed. Mortality losses due to hunting account for almost all of the post-fledging losses in these Canada geese. Since mortality estimates based on banding data indicated a declining population for which there is contrary evidence, some simple population models were constructed and discussed using some known information.

Further research will be necessary before population parameters such as nest desertions and the impact of brood mixing are understood. Physical condition, age, experience, dominance status and family lineage of males and females should be monitored to evaluate the importance of these factors in nest desertions and brood mixing.

MANAGEMENT NOTES AND RECOMMENDATIONS

1. A very small percentage of the potential brood-rearing area is currently being used indicating there is room for many more breeding geese.
2. There is a shortage of suitable secure island-type brood roosting areas and this has probably resulted in significant losses of goslings to coyotes in some years.
3. Provision of additional nesting sites, either suitable artificial structures or earth-fill type islands, away from the current nesting islands would increase the production of Canada geese at Dowling Lake.
4. Brood mixing does not appear to have any negative effect on this population and may have some positive benefits as outlined.
5. If the encroachment of gulls on the shrubby vegetation on the large island is not stopped, there will likely be a resultant decrease in nesting density and production of Canada geese at Dowling Lake. Gulls are also decimating duck production on the lake.
6. Although both mixed and single broods are fragmented during banding operations, they regroup quickly and are back together within a couple of days.
7. Banding data indicates the central Alberta population should be declining but all other indicators show that it is doing very well both at Dowling Lake and in the surrounding area. Therefore, banding data must be used very cautiously.
8. Brood mixing behavior is such that transplant goslings up to 15 days of age will be accepted into resident broods. Broods with goslings up to 21 days still accepted strange goslings into their broods. How

this acceptance might vary between dense-nesting geese and dispersed-nesting geese is not known. Further experimentation is required.

9. Use of artificial platforms on nesting islands already used by geese should be discouraged. However, nest baskets, used in conjunction with natural shrubs or trees, may provide additional useful nest sites not otherwise available to geese.
10. Establishing shrubby cover on islands currently covered with short grasses will probably increase nesting densities.
11. Color marking waterfowl broods, using techniques described in Appendix I, should proceed with the caution that it will cause embryo mortality.
12. Attempts should be made to find the molting areas for subadults and unsuccessful breeders of the Canada goose in the western states and provinces so these areas can be given adequate protection as development proceeds in the north.

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APPENDIX I

Color Marking Canada Goose Goslings at Dowling Lake In 1971 and 1972

Introduction

The technique of using dyes, injected into eggs, to mark the broods of waterfowl was first described extensively by Evans (1951) although he was not the first to use it. This technique marks the hatchling and causes minimal disturbance to the female. The brood can thus be distinguished and followed after hatching. Evans' (1951) publication remains the authority on this technique because, even though it has been widely used since 1951 by others, their results have been rarely published. Evans (1951) reported at least 70 percent hatching success among 79 fertile duck eggs that he had injected with dyes. He recorded no behavioral abnormalities in the dyed ducklings. More recently Titman (pers. comm.) reported mortality rates as high as 16 percent in dye-injected eggs of mallards. Although this technique has been widely used with ducks, I am unfamiliar with any published reports describing modification of the technique for use with Canada goose eggs.

I felt that this technique would be useful for marking individual broods or groups of broods of Canada geese at Dowling Lake. Having individual broods or groups of broods recognizable enables one to study more effectively such aspects as brood movements, interactions with other broods, creching and mortality within broods. The technique was used on Canada geese at Dowling Lake during the 1971 and 1972 breeding seasons. Here I discuss the effects of using this technique on the Dowling Lake goose population.

Methods

I followed the method of injection described by Evans (1951) for injecting duck eggs, but the following modifications were made for the goose eggs.

The number of days incubation, if not known, was estimated by floating the eggs in water. When the eggs had reached an incubation age greater than 24 days, I considered them ready for injection. The eggs were removed from the nest and a hole was drilled 1 to 2 cm from the small end of the egg. The drill consisted of a pin slightly larger than #22 gauge hypodermic needle used for injection. The pin, sticking about 3 mm through a #9 rubber stopper was sterilized using an alcohol swab before each drilling. The dyes were sterilized (15 minutes in a pressure cooker) and stored in 50 ml serum bottles. After swabbing the rubber caps of the serum bottles with alcohol, the appropriate amount of dye was withdrawn using a 1 cc disposable syringe and #22 gauge disposable needle. New needles were used for each egg and a new syringe was used for each clutch of eggs. The tip of the needle was placed into the hole about 3 mm at such an angle as to have the tip pointing toward the small end of the egg, and the dose was injected slowly (5 - 10 sec/egg) into the egg. The needle was withdrawn, the hole was sealed using a small dab of sealant and the egg was placed back in the nest. The sealant used was Dow Corning Silicone Bathtub Caulk as recommended by Lewin (pers. comm.) after he had tested the compound on Japanese quail (Coturnix coturnix) eggs and white leghorn chicken (Gallus domesticus) eggs. This sealant was used because it dries quickly, is water resistant, remains flexible through a wide temperature range and is non-toxic. When all eggs in a clutch had been injected, the nest was covered with down and nesting material. This procedure was used

for each nest in which the eggs were marked. The period of disturbance on the nesting colonies at Dowling Lake was restricted to about one hour per visit allowing a maximum of 10 nests to be completed.

The technique as described was first used on Canada geese at Dowling Lake during the 1971 breeding season. All the eggs from elevated nests (two in old heron nests and eight in artificial nesting platforms) were injected with Ponceau S (red) at a concentration of 6 g/100 ml water. The dosage was 2.2 ml/egg and 59 eggs were marked. It was hoped that goslings from these nests would still be recognizable 6 weeks later when they could be marked permanently. In this way it would have been possible to determine if these progeny showed greater selection for elevated nest sites when breeding in subsequent years. A summary of the clutches injected appears in Table 1. High embryo mortality caused by use of this technique led to experimental testing of chicken eggs early in 1972.

Different concentrations and different dosages of several dyes were injected into 19-day white leghorn chicken eggs. The same procedure as outlined previously for the goose eggs was used except that the chicken eggs were hatched in an incubator. A summary of the dyes used, concentrations and dosages and the number of eggs injected appears in Table 2. The purpose of the experiment was to determine which dyes at which concentration and dosage gave the least mortality along with the best down coloration. Discovery of a procedural mistake (the dye was too concentrated and the dosage was too high) in the 1971 goose egg injections that could be corrected and the high hatching success of the experimental chicken eggs led to the use of the technique again on goose eggs at Dowling Lake during the 1972 breeding season.

Table 1. Hatching success of Canada Goose eggs at Dowling Lake in 1971 after the eggs had been injected with a dose of 2.2 ml/egg of Ponceau S at a concentration of 6 g/100 ml water.

Nest Number	Clutch Size	Hatchable Eggs[a]	Number of Young Leaving the Nest	Number of Eggs Not Hatched With Embryos Older Than 24 Days	Number of Dead Young In the Nest
71-52	6	6	0	6	0
71-10	7	6	0	5	1
71-41	6	6	0	6	0
71-17	5	5	2	1	2
71-62	6	6	1	5	0
71-48	9	4	0	1	3
71-34	7	7	0	7	0
71-91	5	3	3	0	0
71-96	3	3	0	3	0
71-97	5	5	4	0	1
TOTAL	59	51 (87)[b]	10 (17)	34 (58)	7 (12)

[a] The term hatchable means those eggs producing young or having dead embryos older than 25 days.

[b] Percent of the total number of eggs in the 10 clutches.

Table 2. Hatching success of White Leghorn Chicken eggs experimentally injected with embryo colouring dyes in 1972.

Dyes	Concentration	Dosage (ml/egg)	Number of Eggs Injected	Number of Viable Young Produced	Number of Eggs Not Hatched With Embryos Older Than 19 Days
Food Dyes	(% of conc. solution)				
Green	100	0.15	3	2	0
Green	10	0.15	3	3	0
Green	10	0.5	6	6	0
Red	100	0.2	3	1	1
Red	100	0.5	3	2	0
Red	10	0.5	3	3	0
Blue	100	0.2	3	3	0
Blue	10	0.2	3	2	0
Blue	10	0.5	6	6	0
Black	100	0.5	3	1	1
Biological Stains	(g. Stain/100 ml H_2O)				
Fast Green (FCF)	3.8	0.2	3	2	1
	0.038	0.5	3	2	0
Brilliant Blue	4	0.2	3	2	0
	0.08	0.5	3	3	0
Ponceau S	1.2	0.3	6	6	0
	0.12	0.5	3	2	1
Water	Distilled	0.15	3	3	0
		0.45	2	2	0
TOTALS			62	51 (82)[a]	4 (6)

[a] Percent total number of eggs experimentally injected.

All the viable eggs from 37 nests were injected with "Food Club" concentrated liquid color produced by Scott-Bathgate Ltd., Winnipeg, Toronto, Vancouver, Canada. The dyes were injected at dosages of 1 ml/egg for blue, green, purple and brown and 1.5 ml/egg for red as recommended by Titman (pers. comm.). These amounts were increased to about 2 ml/egg if the eggs were pipping because Brace (pers. comm.) said amounts did not seem critical after the egg membranes were broken and that more dye was needed to get an even color distribution at this time. A summary of the clutches injected appears in Table 3.

All statistical cohorts were considered significantly different if $P < 0.05$. A 2 x 2 Chi Square test for independence was used.

Results

The results of the 1971 injections are summarized in Table 1. Embryonic death, infertility and predation caused a 13 percent loss of all the eggs leaving 51 eggs potentially hatchable. Prehatch embryo mortality among those older than 24 days occurred in 67 percent of these eggs and immediate posthatch gosling mortality (died in the nest) occurred with 14 percent of them. Thus 19 percent of the hatchable eggs injected with dye produced viable goslings leaving the nest, whereas 99 percent of the hatchable eggs not injected produced viable goslings leaving the nest.

The results of the experimental injection of white leghorn chicken eggs are summarized in Table 2. The results show that 82 percent of all the eggs injected produced viable young. The average for all eggs in the hatchery varies between 80 and 85 percent. Embryonic death and infertility

caused 11.5 percent loss of all injected eggs leaving only 6.5 percent due to some other cause. There was no significant difference between hatchability of dye-injected eggs and uninjected eggs. The experimental injections also showed that concentrated food-coloring dyes produced better colored down in most cases.

Results of the 1972 injection of Dowling Lake goose eggs appear in Table 3. There were five unsuccessful clutches and 32 successful (producing at least one young leaving the nest). The five unsuccessful nests were all abandoned. It is not known whether they were abandoned because of observer disturbance, territorial abandonment as described by Ewaschuk (1970), failure of the eggs to hatch because of injection or some other factor so they will not be considered further in the following discussion. The number of hatchable eggs was 77 percent of the total number laid in the marked nests in 1972 as compared to 89 percent for 48 known nests in 1971. The percentage of all eggs laid that produced young leaving the nest was 64 in 1972 and 88 in 1971; among hatchable eggs these percentages were 83 in 1972 and 99 in 1971. There was no significant difference between the proportions of the total number of eggs laid that were hatchable in 1972 and previous years, but there was a significantly lower proportion of hatchable eggs producing young leaving the nest in 1972 than in previous years (1967 - 1971). There was no significant difference in hatchability between any of the colors used in the injections; however, the biological significance of this is open to question because of small sample sizes.

Red and green produced well colored broods visible at 0.5 km or more with a 30X spotting scope. The colors remained easily distinguished up to 2 weeks of age, thereafter becoming less obvious until they

Table 3. Hatching success of Canada Goose eggs at Dowling Lake in 1972 after the eggs had been injected with concentrated food coloring dyes.

Nest Number	Clutch Size	No. of Hatchable Eggs	Color Injected	No. of Young Leaving the Nest	No. of Eggs Not Hatched With Embryos Older Than 24 Days	No. of Dead Young in the Nest
72-3[a]	2	2	Red	0	2	0
72-8[a]	3	2	Red	0	2	0
72-10[a]	4	4	Red	0	4	0
72-34[a]	4	4	Red	0	4	0
72-62[a]	4	4	Red	0	4	0
72-7	8	5	Green	5	0	0
72-12	5	5	Green	5	0	0
72-21	5	3	Red	2	1	0
72-24	7	7	Green	7	0	0
72-32	6	1	Blue	1	0	0
72-44	6	4	Red	2	2	0
72-45	6	5	Blue	2	0	3
72-46	6	5	Blue	4	0	0
72-47	10	6	Brown	2	3	1
72-49	6	4	Green	4	0	0
72-51	5	4	Purple	4	0	0
72-54	5	5	Red	2	3	0
72-59	7	4	Blue	2	0	2
72-61	6	5	Blue	2	3	0
72-63	6	4	Brown	4	0	0
72-64	2	2	Red	2	0	0
72-77	5	4	Red	2	2	0
72-78	5	2	Red	2	0	0
72-80	6	5	Blue	5	0	0
72-83	8	2	Blue	2	0	0
72-84	8	6	Green	6	0	0
72-86	6	5	Green	5	0	0
72-88	5	5	Red	5	0	0
72-89	5	5	Blue	5	0	0
72-92	5	5	Red	5	0	0
72-97	5	5	Red	5	0	0
72-108	7	7	Green	6	1	0
72-110	7	7	Green	5	2	0
72-111	5	5	Red	5	0	0
72-113	6	5	Brown	5	0	0
72-115	4	4	Red	3	0	1
72-116	6	5	Red	4	0	1
TOTALS	189	146 (77)[b]		121 (64)	17 (9)	8 (5)

[a] These 5 nests were abandoned for unknown reasons so they are not included in the totals and percentages.

[b] Percent of the total number of eggs in the 32 nests.

could no longer be distinguished after about 4 weeks. Gradual fading of the color and loss of the natal down contributed to the loss of color. Brace (pers. comm.) said that the color may still be visible at banding age (7 to 8 weeks) on down under the wings and on the nape but there was no evidence of this at Dowling Lake. Blue produced well colored broods but they were unsuitable as they could only be distinguished from green at very close ranges (less than 50 meters). Purple and brown marked clutches did hatch but these broods were never observed. Since all the green, red, and blue broods were accounted for, it seems likely that the brown and purple dyes did not mark the broods sufficiently to produce visible colors.

Discussion

The poor hatching success in the 1971 dye injected eggs likely was due to an error in technique when 2.2 ml/egg of Ponceau S at a concentration of 6 g/100 ml water were used instead of 1.5 ml/egg at a concentration of 1.2 g/100 ml water. The error resulted when Ponceau S and Ponceau SX were assumed the same when in fact they were not. Correction of this mistake reduced mortality from 81 percent in 1971 to 17 percent in 1972 at Dowling Lake.

The 82 percent hatching success of experimentally injected white leghorn chicken eggs did not differ from the 80 to 85 percent hatching success normally expected in uninjected hatchery eggs. Thus very little or no mortality could be attributed to the injection procedure in chicken eggs.

The data on injected goose eggs from 1972 indicate clearly that significant unaccountable mortality occurred that most likely was due to

the use of the embryo dyes. The reason why the injection technique causes both additional prehatch and posthatch mortality is unknown. It seemed to retard the growth of some embryos making them fall behind the others in development just enough so that they did not hatch or were left behind when the rest of the brood left the nest. In other cases the embryos seemed to die at the time of injection. No evidence of injury to the dead embryos themselves was found but in some cases there was bleeding from ruptured vessels in the yolk sac circulation that may have caused death.

The dyed broods allowed individual identification of goslings and made it much easier to study various aspects of brood behavior such as creching. There was no evidence of any obvious behavioral abnormalities among colored goslings. There was no rejection of colored goslings by the parent geese. Red, green and normal goslings were present in one mixed brood and two colors were present in three other mixed broods indicating that there was no discrimination against goslings colored different than the broods the pairs had hatched themselves. Colored goslings were not disproportionately involved in the brood mixing of the geese. The effect of removing 17 percent of the potential goslings from the population was not known but may be serious if the technique was used over a period of several years, however, there may be a surplus in this population in which case this mortality would not reduce the subsequent breeding populations, just the annual production.

Summary

Poor hatching success of Canada goose eggs at Dowling Lake during the 1971 breeding season, after injection of the eggs with an embryo dye,

was attributed to an error in dye concentration. Correction of this error and refinement of the technique increased the hatching success significantly from 19 percent in 1971 to 83 percent in 1972, however, hatching success was still significantly lower than the 99 percent expected success based on previous years data. The increased mortality is thus correlated with the use of the injection technique but the cause of this mortality is not known.

Marked broods facilitated better observation of brood behavior. There is no evidence that the colored goslings exhibited abnormal behavior. The effect of the increased mortality on the Canada goose population of Dowling Lake is unknown.

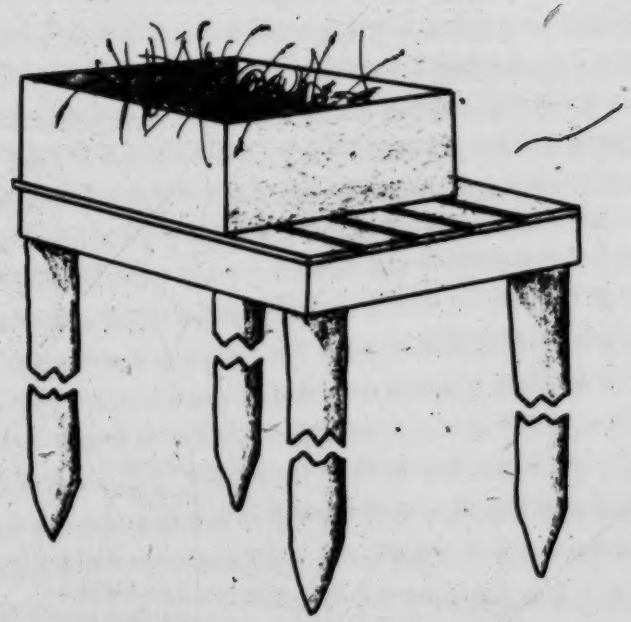
Literature Cited

Evans, C. D. 1951. A method of color marking young waterfowl. J. Wildl. Manage. 15:101-103.

Ewaschuk, E. 1970. The influence of territorial behavior on nesting success in a population of Canada geese. M.S. Thesis. Univ. of Alberta, Edmonton. 60 pp.

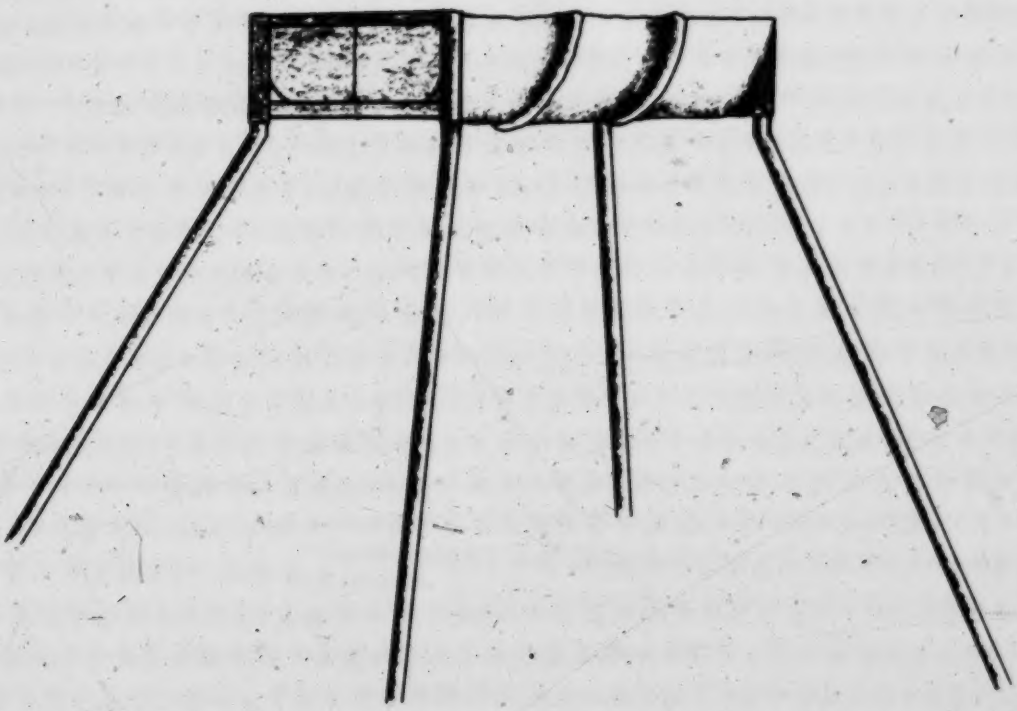
APPENDIX II

Artificial Nesting Platforms at Dowling Lake



A. Wooden Nesting Platform

The platform deck consisted of a 91 cm square frame (5.1 x 10.2 cm boards) with five 2.5 x 10.2 cm boards nailed on top. The nesting box was a 61 cm square frame (2.5 x 15.2 cm boards) nailed to the deck. The deck and nesting box were supported by four treated, round fence posts (10.2 cm in diameter and 4.7 m long). The posts were pounded about 25 cm into the ground with a tractor driven post driver, and the decks were nailed on top. Straw bales, marsh vegetation or wood chips were used as nesting material.



B. Metal Nesting Platform

The metal split drum nesting platform illustrated above is described in the following reference: Rienecker, W. C. 1971. Canada goose nesting platforms. Cal. Fish Game 57:113-123.